

## EARLY CRETACEOUS FROGS FROM MOROCCO

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## ABSTRACT

The Lower Cretaceous Moroccan locality of Ksar Met-Lili near Anoual has yielded a diverse microvertebrate assemblage including mammals, small reptiles, and amphibians. Here the frogs are described for the first time. Although the material is fragmentary, iliac structure, supplemented by other cranial and postcranial elements, demonstrates the presence of two distinct taxa. One genus is interpreted as a discoglossid, related to members of the Jurassic North American genus *Enneabatrachus*. The second frog represents a new taxon, and is here named *Aygroua anoualensis*. It is more difficult to classify, but attributed procoelous vertebrae and a specialized premaxillary-maxillary overlap suggest it is probably a mesobatrachian, possibly a basal pipimorph.

KEY WORDS: Frogs, Anura, Anoual, Lissamphibia, Cretaceous, Morocco

## INTRODUCTION

Frogs and toads (Anura) form a large and successful group of tetrapods, with over 4000 living species distributed globally except for polar areas (Stebbins and Cohen, 1995). Traditionally (e.g., Duellman, 1975), frogs were divided between the Archaeobatrachia (*Ascaphus*, *Leiopelma*, discoglossids, pipoids, and pelobatoids) and the Neobatrachia (all derived frogs including ranids, bufonids, and hylids). However, most more recent authors (e.g., Laurent, 1979; Ford and Cannatella, 1993; Hillis et al., 1993; Henrici, 1994, 1998*a,b*; Trueb, 1996; but see Hay et al., 1995; Hedges and Maxson, 1993; Gao and Wang, 2001) recognize Mesobatrachia as the sister group of Neobatrachia, with a morphology somewhat intermediate between that of basal frogs and higher taxa (Fig. 1). Mesobatrachian and neobatrachian frogs together form the Pipanura (Ford and Cannatella, 1993). Mesobatrachia (sensu Ford and Cannatella, 1993) includes two major clades—the Pelobatoidea (pelobatids [including megophryines], and pelodytids) and the Pipoidea (rhinophrynids, pipids, and the extinct palaeobatrachids). Within the Pipoidea, pipids and palaeobatrachids are sister taxa (forming the Pipimorpha of Ford and Cannatella, 1993). Gao and Wang (2001) recently proposed a very different arrangement whereby pelobatoids were more closely related to discoglossids and Mesobatrachia was paraphyletic. However, their analysis did not include any neobatrachians. In this paper, we have kept to the more widely accepted phylogeny of Ford and Cannatella (1993).

The fossil history of frogs extends back into the Early Triassic, with the stem salientians *Triadobatrachus* (Madagascar, Rage, and Roček, 1989) and *Czatkobatrachus* (Poland, Evans, and Borsuk-Bialynicka, 1998). There is then a considerable hiatus before the first records of crown-group anurans in the Early Jurassic (*Vieraella*, Argentina, Reig, 1961;

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Submitted 24 January 2002.

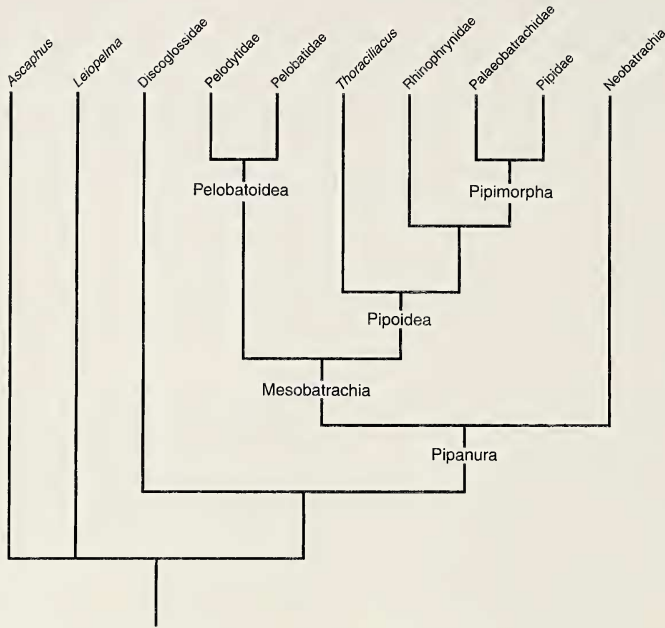


Fig. 1.—Phylogenetic relationships of major anuran groups. The Early Cretaceous genus *Thoraciliacus* has been added since it features in the discussion. Based mainly on Ford and Cannatella, 1993 and Trueb, 1999.

*Prosalirus*, USA, Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). Discoglossids are first recorded from the Middle Jurassic (Evans et al., 1990), pipoids and pelobatoids from the Late Jurassic (Evans and Milner, 1993; Henrici, 1998*a, b*; Sanchíz, 1998), and neobatrachians from the Late Cretaceous (leptodactylids, Báez and Peri, 1989). However, our knowledge of the Mesozoic record of Gondwana remains limited. In Africa, Mesozoic frogs are extremely rare. Frog remains have been recorded, but not described, from the Early Cretaceous of Cameroon (Congleton, 1988; Flynn and Brunet, 1989) and Malawi (Jacobs et al., 1990), whereas in the Late Cretaceous, pipoids and other frogs are known from Niger (Broin et al., 1974; Báez and Rage, 1998), the Sudan (Werner, 1994; Evans et al., 1996), Madagascar (Asher and Krause, 1998), and South Africa (Haughton, 1931; Estes, 1977).

The Moroccan microvertebrate locality of Ksar Met-Lili (Anoual) is situated in the Eastern High Atlas Mountains, 100 km east of the city of Anoual. This basal Cretaceous outcrop has produced an important and diverse assemblage of mammals (Sigogneau-Russell, 1988, 1991*a, b*, 1992, 1995) as well as other small vertebrates (Sigogneau-Russell et al., 1990, 1998), including sharks (Duffin and Sigogneau-Russell, 1993), lizards (Richter, 1994; Broschinski and Sigogneau-Russell, 1996), two taxa of sphenodontian (Evans and Sigogneau-Russell, 1997), and several amphibians, including albanerpetontids, caecilians (Evans and Sigogneau-Russell, 2001) and the frogs described here.

#### GEOLOGY AND MATERIAL

The 'couches rouges' of the High Atlas form a continuous sequence from Middle Jurassic (Bathonian) to Lower Cretaceous (Aptian) (Sigogneau-Russell et al., 1990). Microvertebrate material comes from a calcareous lens about 0.2 m thick and covering an area of roughly 200 m<sup>2</sup>. This lens represents a continental deposit intercalated between marine beds, and has been

interpreted as forming part of a deltaic sedimentary environment close to the sea. Analysis of the calcareous nannofossils (holococcoliths) suggests a basal Cretaceous (Berriasian) age for the assemblage as a whole (Sigogneau-Russell et al., 1990; Duffin and Sigogneau-Russell, 1993). Vertebrate remains are small and completely disarticulated. The bones are frequently broken, but appear to have been deposited under relatively quiet conditions since they show little evidence of either polishing or abrasion.

The frog material falls into two distinct morphotypes demonstrating the presence of two discrete taxa. On the basis of comparisons with modern material, the Anoual frogs were relatively small, with a snout-vent length of around 45 mm (35–60 mm). Only a minority of elements represent the upper size range, suggesting that most Anoual frogs were immature at death. This is supported by the weak ossification of all but a few of the vertebral articulations.

#### METHODOLOGY

Frog bones are highly distinctive in their morphology, and there is little possibility of confusion with the bones of other tetrapods. Anuran osteology has also been comparatively well studied (e.g., Lynch, 1971; Trueb, 1973, 1993). The Anoual frog material consists of around 200 individual fragments representing fifteen different skeletal elements, the most common being presacral vertebrae, maxillae, and ilia. The ilium is generally considered to be the most characteristic and easily recognized anuran element in microvertebrate assemblages (e.g., Sanchíz, 1998), and ilia are frequently used as holotypes. At Anoual, the presence of two distinct iliac morphologies signals the presence of two distinct taxa, a conclusion supported by the recognition of two morphotypes for almost every other skeletal element represented. However, since the Anoual frog material is fragmentary and completely disarticulated, the task of matching skull, vertebral, and limb elements with the individual iliac types is not straightforward, particularly when the two frogs are of similar size, are mostly immature, and may have been present in comparable numbers.

One of the two iliac types closely matches that of basal discoglossid frogs from several Jurassic and Early Cretaceous localities in Europe and North America. The other lacks obvious discoglossid characters and apparently belongs to a different anuran group. In the descriptions that follow, the cranial and postcranial elements that show the closest resemblance to known elements of basal discoglossids (e.g., the Middle Jurassic *Eodiscoglossus oxoniensis*, Evans et al., 1990) are tentatively associated with the first iliac type. Those elements showing a different morphology are described with the second frog. It must be stressed, however, that these attributions are provisional and speculative; they have not been used in taxon diagnoses. In some instances, for example the Type 2 premaxillae and maxillae, there is direct evidence of association in the form of overlap surfaces. In many other cases, as outlined in the discussion section that follows, it is the combination of features from different attributed elements that strengthens the argument.

Institutional abbreviations appear as follows: AMNH, American Museum of Natural History; MCM, Muséum national d'Histoire naturelle, Paris, France.

#### SYSTEMATIC PALEONTOLOGY

Anura Rafinesque, 1815

Discoglossidae Gunther, 1859

*aff. Enneabatrachus* sp. Evans and Milner, 1993

(Fig. 2A–G)

*Attribution.*—The general iliac morphology of the Type 1 Anoual frog matches that of discoglossid frogs as characterized by Estes and Sanchíz (1982a) and Sanchíz (1998)

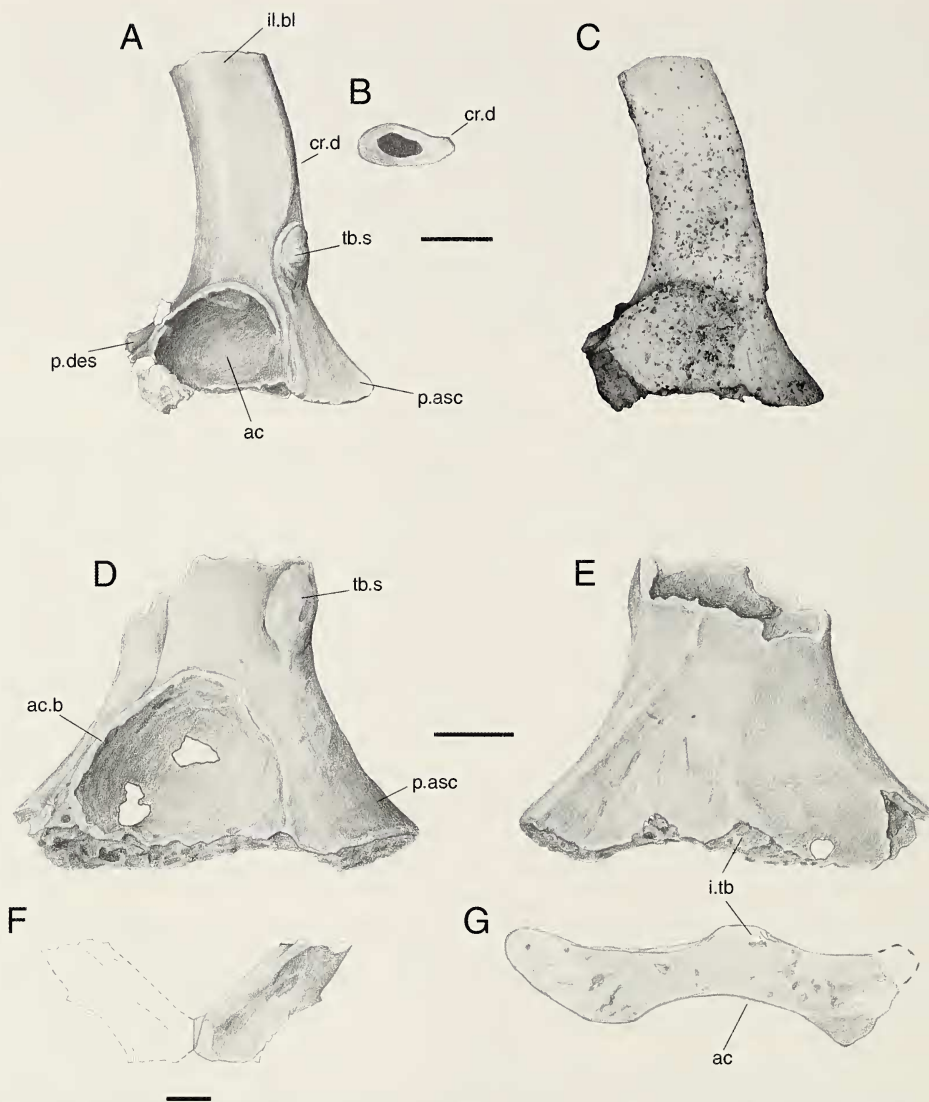


Fig. 2.—aff. *Enneabatrachus*, ilium. A–C, MCM 60, holotype left ilium in A. Lateral, B. Shaft cross-section, C. Scanning electron micrograph, lateral view. D–G, MCM 59, Paratype left ilium, in D. Lateral view, E. Medial view, F. Ventral view to show approximate angle of articulation based on alignment of the interiliac tubercle, and G. Cross-sectional views. Scale bars = 1 mm. White areas are matrix.

(large ovoid dorsal tubercle, well-developed processus ascendens), and broadly resembles that of several known taxa recovered from Jurassic and Early Cretaceous localities (e.g., *Enneabatrachus*, Evans and Milner, 1993; *Eodiscoglossus oxoniensis*, Evans et al., 1990; *Paradiscoglossus*, Estes and Sanchíz, 1982b; unnamed Japanese form, Evans and Manabe, 1998). It differs from the living *Bombina* and *Barbourula*, and the Cretaceous *Scotiophryne* (Estes, 1977), in having a prominent tuber superior; from *Discoglossus*, *Paradiscoglossus*, *Wealdenbatrachus* (Fey, 1988) and described species of *Eodiscoglossus*

(Hecht, 1970; Vergnaud-Grazzini and Wenz, 1975; Evans et al., 1990) in the absence of a pronounced dorsal crest and of a supraacetabular fossa; and from *Enneabatrachus hechti* and *Eodiscoglossus* in the presence of an interiliac tuber, however weak. However, in terms of general blade shape, position and size of the tuber superior, absence of a supracetabular fossa, the shape of the acetabulum (smoothly rounded) and some extension of the ventral acetabular rim, the closest similarity is between the Anoual form and the Late Jurassic Morrison *Enneabatrachus hechti* (Evans and Milner, 1993). The main differences are the apparent absence of an interiliac tuberosity in *Enneabatrachus hechti*, a greater degree of ventral expansion of the acetabular rim, and a greater dorsal extension of the tuber superior beyond the margin of the bone, such that there is a distinct dorsal prominence in medial view, a feature not seen in the Anoual form. Very little work has been done on intra- and interspecific variation in frogs, but considerable interspecific differences can occur in the size and shape of the tuber superior and dorsal prominence (see figures in Sanchíz, 1998; MJ/SE personal observation), and there are differences in blade shape between *Eodiscoglossus oxoniensis* and *E. santonjae* (SE personal observation).

### Description

*Ilium*.—The Type 1 ilium is represented by 13 specimens, the most informative of which are MCM 59 and MCM 60 (Fig. 2A–G). The acetabulum is shallow with a relatively unexpanded acetabular rim (Fig. 2A, C, D), although the ventral margin is deeper than the dorsal one. There is a short, flared pars ascendens that expands medially to form a buttress-like ridge, but the pars descendens is not significantly developed. Medially, there is a weak centrally placed interiliac tuberosity (Fig. 2E, G), and the two ilia would meet at an angle estimated as roughly 90° (Fig. 2F). The acetabular region grades smoothly into the iliac blade, with the latter never less than one-half the basal width. The iliac blade is ovoid in cross-section (Fig. 2B). There is a small dorsal crest, but this is poorly demarcated from the rest of the blade. The crest is certainly less developed than that of the Type 2 ilium, even though all specimens of the latter are of smaller overall size. The tuber superior is prominent (Fig. 2A, D), but does not extend beyond the dorsal margin of the bone. Its long axis is directed anteriorly.

*Premaxilla*.—The premaxillae are paired dermal bones that form the most anterior part of the maxillary arch (Trueb, 1973). Anoual premaxillae all have 16–21 tooth positions and a short, moderately wide, parallel-sided alary process (roughly a third of the total labial width) containing a recess for the anterior end of the nasal cartilage (Figs. 3B, E). Both types have bicuspid, pedicellate teeth (Fig. 3G–H), but they differ in the form of the alary process and that of the pars palatina.

Type-1 premaxillae (e.g., MCM 62, Fig. 3A–C) have an alary process that is more sharply angled (45°) posteriorly. There is a small but prominent tubercle at the labio-medial base. This is present on even the smallest Type 1 specimens (e.g., MCM 63) and thus seems to be characteristic of this premaxillary type. The pars palatina is narrowest at its mid-point while medially it extends back into a lanceolate projection. The exaggerated medial curve of this projection results in the formation of a notch (n, Fig. 3A) where the pars palatina meets the vertical pars dentalis. The lateral margin of the pars palatina also expands but to a smaller degree, and is marked by a series of ridges, grooves, and tubercles that give it a roughened, convoluted appearance. This premaxillary type lacks any overlap surface for the maxilla, and the two bones presumably abutted.

*Maxilla*.—Numerous maxillary fragments occur amongst the Anoual material and most conform to a single type (Type 1). A second kind (Type 2, see below) is known only from

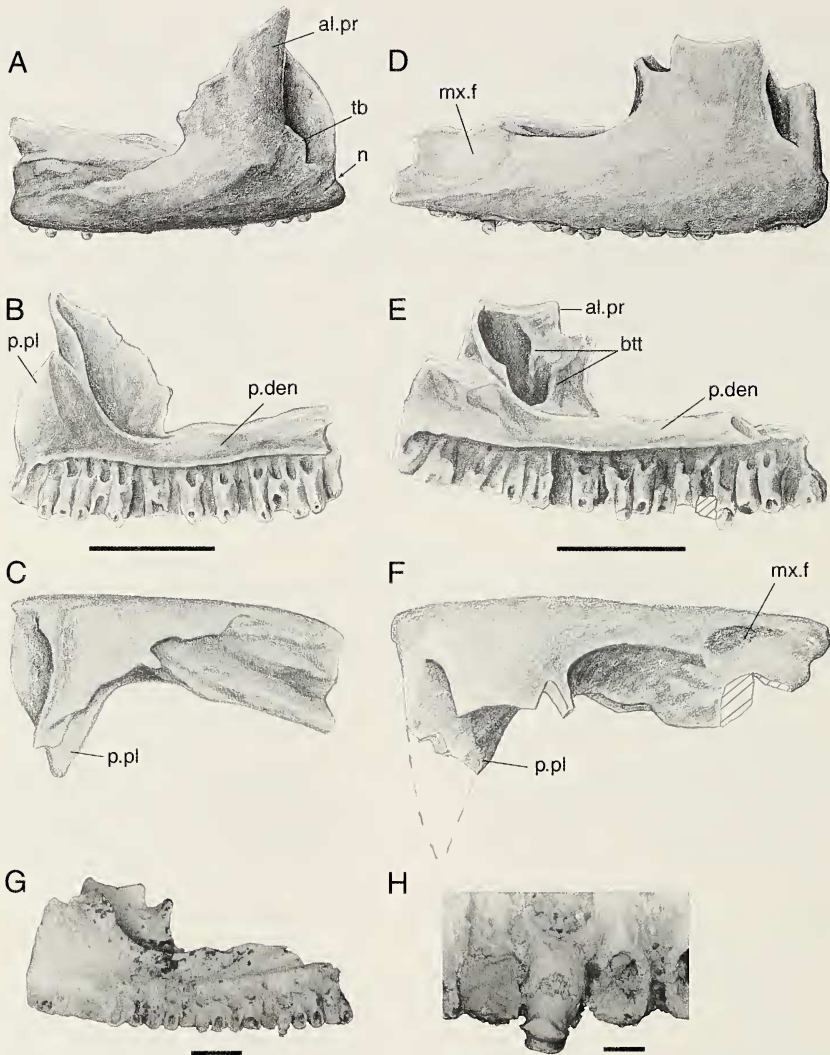


Fig. 3.—Anoual anuran premaxillae. A–C, MCM 62, Type 1 right premaxilla in A. Labial, B. Lingual, and C. Dorsal views. D–F, MCM 61, Type 2 right premaxilla in D. Labial, E. Lingual, and F. Dorsal views. G–H, Scanning electron micrographs of MCM 61, with G. Lingual view, H. Enlargement to show pedicellate bicuspid tooth. Scale bars = 1 mm except G (0.5mm) and H (0.1mm). Hatched areas are regions of broken bone.

anterior and posterior fragments and differs primarily in having larger anterior teeth and a groove on the labial surface. Neither type bears dermal ornament.

Type 1 (Fig. 4A–F) is represented by sufficient specimens (e.g., MCM 64, 65, 66) to permit an estimate of around 50–55 tooth positions. The teeth have relatively short circular or ovoid pedicels, the height being no more than two or three times the width. The maxillary rostrum is incompletely known, but the anterior part (MCM 66, Fig. 4D) is labially expanded and lingually concave. Its relationship to the premaxilla is unclear, but, at least as preserved, it lacks an edentulous overlap process, unlike Type 2. Above the tooth row, the crista dentalis is robust and cylindrical in cross-section (MCM 65, Fig. 4B–D),

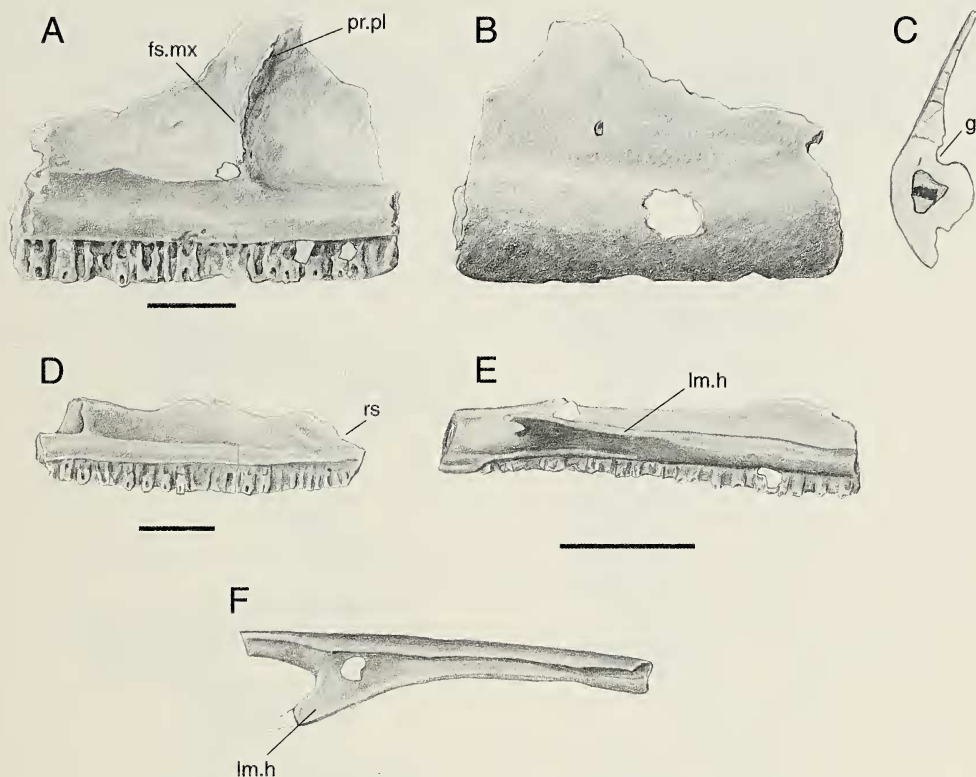


Fig. 4.—Anoual Type 1 anuran maxillae. A–C, MCM 65, central region of a left bone, in A. Medial, B. Lateral, and C. Cross-sectional views. D. MCM 66, anterior region of left bone, medial view. E–F, MCM 64, posterior region of left bone, in E. Medial, and F. Dorsal views. Scale bars = 1 mm. White areas are matrix.

becoming more horizontal posteriorly (as the lamina horizontalis). It terminates posterodorsally by expanding into a barb or fluke-like process (e.g., MCM 64, Fig. 4E, F). The processus palatinus is weakly developed and delimits a posterior cavity, the fossa maxillaris (fs.mx, Fig. 4A). From this cavity a gutter (g, Fig. 4C) runs backward along the dorsal surface of the crista dentalis, expanding posteriorly as the lamina does (Fig. 4E–F). The labial surface of all specimens is smooth and convex.

*Atlas*.—The atlas (cervical of Trueb, 1973) is easily distinguished from other vertebrae by the paired anterior cotyles for articulation with the occipital condyles of the skull. Four atlantal centra, representing two distinct morphologies, have been recovered at Anoual. In both cases, however, the atlantes match the ‘type II’ morphology of Lynch (1971)—the cotyles fully separated, but only by a relatively small gap.

The Type 1 Anoual atlas (MCM 79, 80) is trapezoidal and relatively long (Fig. 5A–E, J). The anterior cotyles are deep and oval, with their long axes inclined dorsolaterally at roughly  $10^\circ$  (Fig. 5A, B). They are fully separated by a slight anterior projection. Posteriorly there is a rounded imperforate cotyle suggesting opisthocoely. The centrum itself is dorsoventrally flattened, with a smooth or pitted ventral surface that might be indicative of immaturity. The neural arches are broken away but the pedicels appear to narrow sharply from a broad base.

*Sacral vertebra*.—Like the atlas, the sacrum is also unmistakable (Fig. 6A–H). Type 1 is represented by four specimens, from both juvenile and fully adult individuals. MCM 83

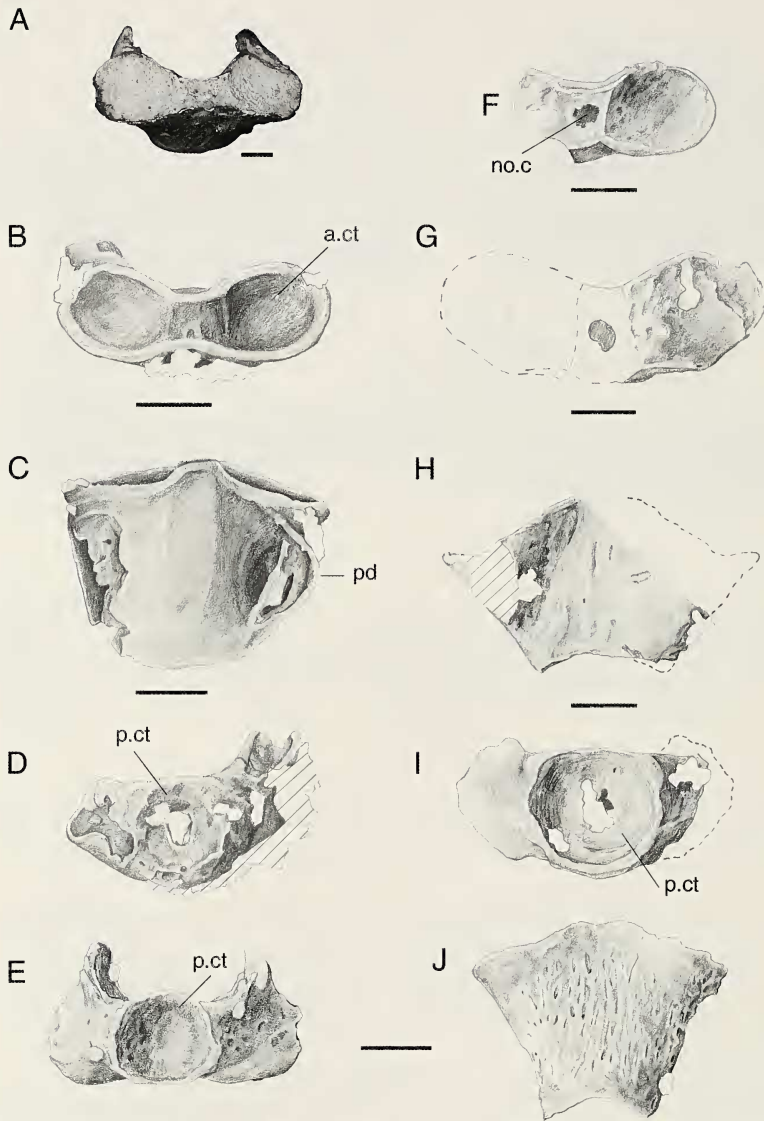


Fig. 5.—Anoual anuran atlantes. A–E, J, Type 1 atlantes, with A. MCM 79, scanning electron micrograph, anteroventral view. B–D, MCM 80, in B. Anterior, C. Dorsal, and D. Posterior views. E, J, MCM 79, in E. Posterior and J. Ventral views. F–I, Type 2 atlantes, F. MCM 82, anterior view. G–I, MCM 81, in G. Anterior, H. Dorsal, and I. Posterior views. Scale bars = 1 mm except A (0.5 mm). White areas are matrix; hatching denotes broken surfaces.

(Fig. 6A–D), an adult sacral, is by far the most complete. It is short, wide, and robust with fully formed joint surfaces, a depressed oval anterior condyle and paired posterior condyles separated by a very small remnant of the notochordal canal (Fig. 6A, B). The last presacral vertebra was thus clearly opisthocoelous or diplasiocoelous (bicotyler). The neural arch is complete, with a thick weakly crested dorsal lamina and robust pedicels supporting strong, posteriorly directed, cylindrical transverse processes and large expanded



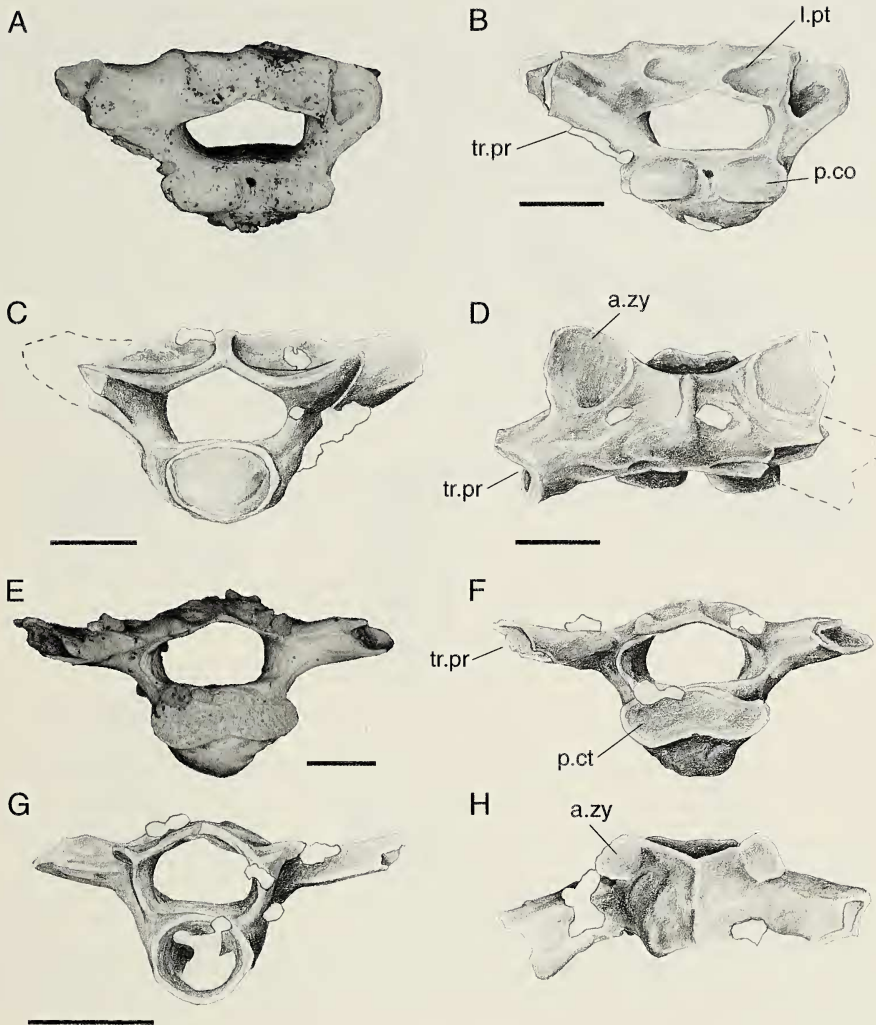


Fig. 6.—Anoual anuran sacra. A–D, MCM 83, Type 1 sacral in A. Scanning electron micrograph, posterior view, B. Posterior view, C. Anterior view, D. dorsal view. E–H, MCM 85, Type 2 sacral, in E. Scanning electron micrograph, posterior view, F. Posterior view, G. Anterior view, H. Dorsal view. Scale bars = 1 mm. White areas are matrix.

anterior zygapophyses. The posterior margin of the arch is straight with paired pits for spinal ligaments. MCM 84 (not figured) is a left vertebral fragment interpreted as a juvenile Type 1. It is notochordal but the posterior surface is clearly divided into discrete articular condyles. There is also no anterior condyle, but the notochordal cotyle bears a raised lateral edge that presumably represents a stage in the development of the adult condyle. Several of the immature presacral centra show a similar condition and can be attributed to this vertebral type (see below).

*Post-atlantal presacral vertebrae.*—The atlantes and sacra together suggest that of the two Anoual frogs, one is opisthocoelous and the other is amphicoelous or procoelous (see below). However, although two morphotypes are present amongst the remaining vertebrae,

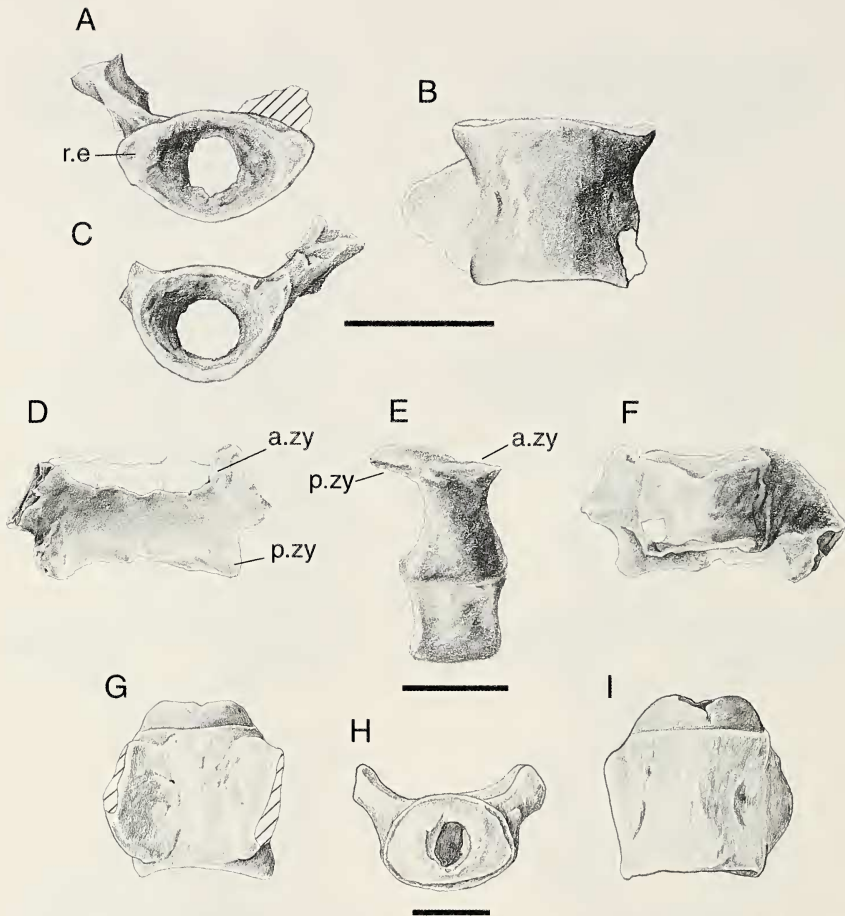


Fig. 7.—Anoual anuran presacrals, Type 1. A–C, MCM 87, Type 1 centrum in A. Anterior, B. Ventral, and C. Posterior views. D–F, abraded Type 1 vertebra, MCM 206, in D. Dorsal, E. Lateral, and F. Ventral views. G–I, MCM 207, in G. Dorsal, H. Anterior, and I. Ventral views. Scale bars = 1 mm. White areas are matrix; hatching denotes broken surfaces.

most of the centra are amphicoelous (Fig. 7A–F, Fig. 11A–B). Either these amphicoelous presacral vertebrae represent additional taxa, or they are immature.

Type 1 amphicoelous vertebrae have centra that are usually wider than long, with short, flat, neural arch laminae (Fig. 7D, E). The relative positions of the zygapophyses and arch margins suggest a degree of imbrication. The transverse processes are rounded in cross-section but usually broken at the base. MCM 78 (not figured) is an exception in preserving more distal parts of the transverse process. A suture line separates the proximal portion of the process from the tip, suggesting that a free rib has become fused. In general morphology, these vertebrae resemble the bicondylar Type 1 sacral, except that they are notochordal and amphicoelous, rather than opisthocoelous. However, they are also closer in size to the juvenile Type 1 sacrum. As noted above, this vertebra (MCM 84) lacks an anterior condyle but has an articular surface with a raised lateral edge. This condition is found in at least some of the Type 1 presacrals (e.g., MCM 87, Fig. 7A, r.e), suggesting

they may also belong to an animal that was opisthocoelous when fully adult. This conclusion is supported by MCM 207, a more mature vertebral centrum bearing an incomplete anterior condyle (Fig. 7G–I). Isolated Type 1 centra closely resemble those previously described for Jurassic and Early Cretaceous discoglossids (e.g., *Eodiscoglossus*, Estes and Sanchíz, 1982a; Evans et al., 1990).

*Scapula*.—The anuran pectoral girdle is adapted to absorb the stress of saltorial locomotion (Trueb, 1973). The scapula is generally short and broad with separate articular surfaces for the clavicle (pars acromialis) and coracoid (processus glenoidalis) divided by a scapular cleft (lost in some taxa, e.g., *Ascaphus*, *Pipa*).

Type 1 scapulae (e.g., MCM 93, Fig. 8A, D, MCM 94, Fig. 8G) have a short broad scapular blade that is mediolaterally flattened. No trace of the anterior margin is preserved. The bone is weakly cleft proximally, with the interglenoid sinus directed mediolaterally. The pars acromialis is thick (mediolaterally) and forms a distinct anterior wall to the scapula cleft. The pars glenoidalis is prominent and faces posteriorly.

Anura Rafinesque, 1815  
Mesobatrachia Laurent, 1979  
Genus *Aygroua*, **new genus**

*Etymology*.—From Ay-grou, a Moroccan Berber word for frog.

*Aygroua anoualensis*, **new species**  
(Fig. 9A–D)

*Etymology*.—From the area of the type locality, Anoual.

*Holotype*.—The proximal part of a right ilium, Muséum national d'Histoire naturelle, Paris, MCM 183.

*Type locality and horizon*.—2.5 km East South East of Ksar Met-Lili, Anoual syncline, 100 km east of the city of Anoual, Talsint Province, Morocco (International coordinates: 3°13'50"W; 32°42'9.5"N); Morocco B sequence of the 'couches rouges', Lower Cretaceous, Berriasian.

*Referred material*.—Ilium MCM 57 and eight further iliac specimens. A number of other skeletal elements are more tentatively assigned to this taxon but do not feature in the diagnosis. These include the following: a premaxilla, MCM 61; maxillae, MCM 67–69; atlantes, MCM 81, 82; a sacral vertebra, MCM 85; presacral vertebrae, MCM 77, 86, MCM 208–210; and scapulae, MCM 95–96.

*Diagnosis*.—Small anuran having an iliac blade with a strong dorsal crest; strong dorsal prominence but no tuber superior; flared ventral acetabular rim which is visible in medial view and obscures pars descendens laterally; and large, ventrally placed interiliac tuberosity supported by a strong medial buttress.

*Remarks*.—*Aygroua* differs from most discoglossids in having an ilium showing the following combination of features: a strong dorsal prominence but lacking the typical ovoid tuber superior; preacetabular narrowing of the iliac blade, and a strong medial iliac sychondrosis (Fig. 9C). *Aygroua* resembles the living discoglossid *Bombina* in the preacetabular narrowing and medial sychondrosis, but differs in the expansion of the dorsal crest and prominence. *Aygroua* differs from *Notobatrachus* (Middle Jurassic, Argentina, Báez and Basso, 1996), *Mesophryne* and *Callobatrachus* (Early Cretaceous, China, Gao and Wang, 2001), and the living *Leiopelma* and *Ascaphus*, in having a strong dorsal crest; differs from pelobatoids in lacking the spiral groove on the dorsal margin of the iliac shaft; and differs from known rhinophrynids (including the basal *Rhadinosteus*, Henrici, 1998b), but resembles pipimorphs, in having a strong interiliac tuberosity. Comparison with the Early Cretaceous pipoids *Thoraciliacus* and *Cordicephalus* (Nevo,

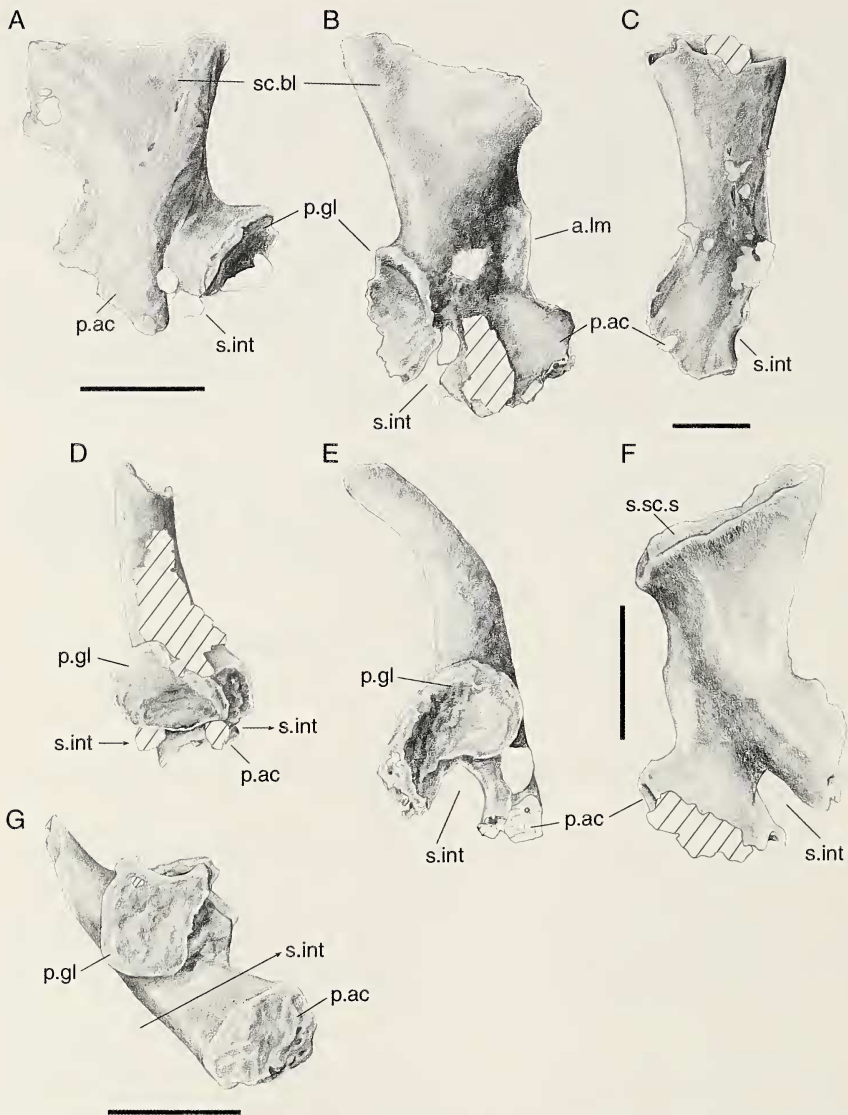


Fig. 8.—Anoual anuran scapulae. A–C, lateral views, with A. MCM 93, Type 1, B. MCM 95, Type 2. C. MCM 96, ?aberrant Type 2. D–E, posterior views of D. MCM 93, and E. MCM 95. F. MCM 95, medial view. G. MCM 94, Type 1 scapula, posterior view to show lateromedial course of scapular cleft. All scale bars = 1 mm, A, B, D and E to the same scale. White areas are matrix; hatching denotes broken surfaces.

1968; Trueb, 1999) is made difficult by the difference in preservation (3-D disarticulated vs. 2-D articulated), and by the lack of detailed information on iliac shape (Trueb, 1999). There are, however, striking differences in, for example, premaxillary, sacral, and urostyle morphology between *Thoraciliacus* and *Cordicephalus* on the one hand (triangular alary process of premaxilla; flared sacral transverse processes; fused postsacrals) and the anuran elements preserved at Anoual (parallel-sided alary processes; unflared or slightly flared sacral transverse processes; no postsacrals).

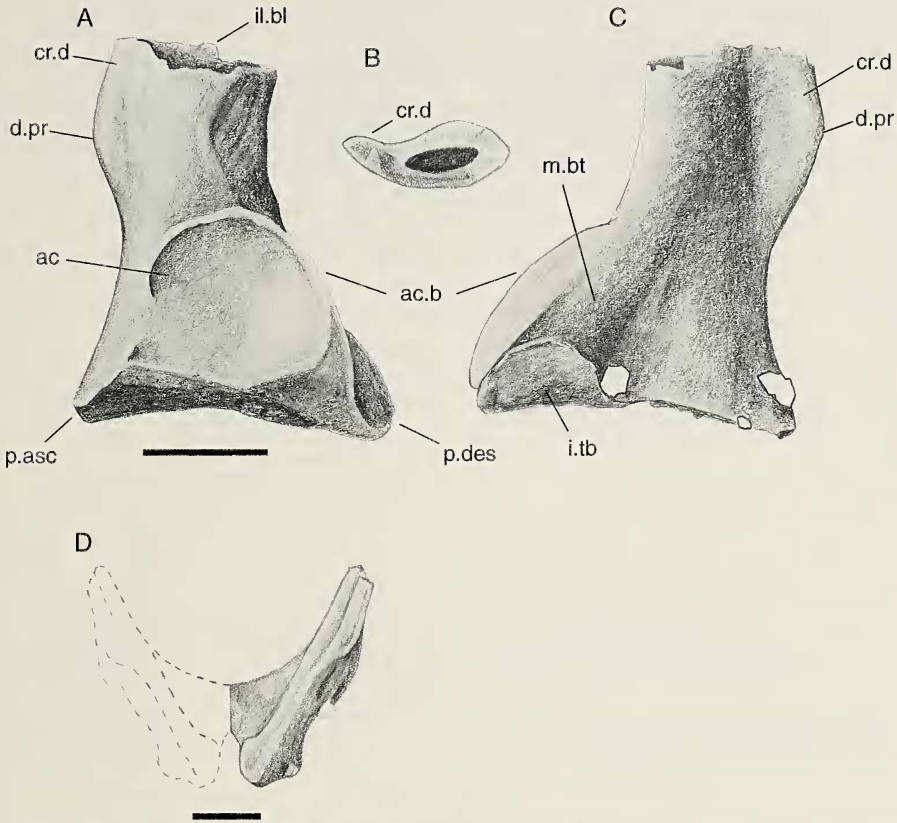


Fig. 9.—*Aygrova anoualensis*, gen. et sp. nov., holotype right ilium, MCM 183, in A. Lateral, B. Cross-section of shaft, C. Medial views, D. Posterior view to show approximate angle of articulation based on alignment of the interiliac tubercle. Scale bars = 1 mm. White areas are matrix.

*Description*

*Ilium*.—The *Aygrova* ilium is represented by nine specimens, the most informative of which are MCM 183 (Fig. 9) and 57. These ilia have a deep asymmetrical acetabulum. The ventral acetabular rim is greatly expanded to the extent that it is visible in medial view and almost completely obscures the pars descendens (Fig. 9A). The pars ascendens is prominent but shows little expansion. The pars descendens is larger and separated from the acetabular rim by a distinct groove. Medially (Fig. 9C), the acetabulum is strengthened by a large posterior buttress leading to the iliac tuberosity, a feature that may be associated with an aquatic lifestyle (Vergnaud-Grazzini and Hoffstetter, 1972). A second, deeper groove separates this buttress from the pars descendens. The buttress significantly increases the size and surface area of the interiliac synchondrosis. The interiliac angle can be estimated at 60° (Fig. 9D).

The iliac blade is relatively slender, but it bears a prominent crest (Fig. 9B, D) that in some specimens accounts for up to half the width of the blade at its most dorsal point. Overall, there is a sharp distinction between the basal, acetabular region of the ilium and the blade, the latter being only about one-third of the proximal width. There is a shallow but elongated dorsal prominence (d.pr) with a thickened margin but no development of

a tuber superior as such (Fig. 9A). The prominence gives the dorsal margin a strong sigmoidal outline.

*Premaxilla*.—The Type 2 premaxilla (e.g., MCM 61, Fig. 3D–H) resembles those of Type 1 in tooth number and general form, and has a smooth, convex labial surface. The alary process has both medial and lateral buttresses. Together these create four sharp edges: medial, posteromedial, lateral, and posterolateral. Between the two medial edges there is a very deep cavity, while the two lateral edges frame a smooth, concave surface that sometimes displays one or two small basal foramina. Lingually, the pars palatina extends back almost horizontally and has a smooth margin. The distal end of the extension is unknown, but the proximal base is less symmetrical than that of Type 1. This premaxillary type has a basin-like lateral overlap surface for the maxilla (mx.f, Fig. 3F).

*Maxilla*.—The Type 2 maxilla is much rarer than Type 1, and is represented only by four anterior fragments (e.g., MCM 67, 68, Fig. 10A–D) and one posterior fragment (MCM 69, Fig. 10E–F). The anterior and posterior fragments are tentatively associated by the presence of a labial groove, although the tooth morphology differs. Anteriorly (Fig. 10A, C), the tooth pedicels are narrow in cross-section, and are relatively taller than those of Type 1. Posteriorly (Fig. 10E), they are shorter and smaller. A similar disparity in tooth size does, however, occur in other known taxa (e.g., *Eodiscoglossus oxoniensis*, Evans et al., 1990). The Type 2 rostrum is lingually convex rather than concave and the labial surface differs from that of Type 1 in having a wide but shallow groove (l.gr, Fig. 10F) on the otherwise flat labial surface (Fig. 10B, D, F). In cross-section, this groove has the effect of shifting the crista dentalis labially, giving the bone the appearance of having a labially expanded margin or skirt. The rostral area also differs in another, potentially more significant, way from Type 1. It has an edentulous anterior premaxillary process (ed. rs, Fig. 10A, B) that matches the facet on the Type 2 premaxilla, suggesting an overlap between the maxilla and premaxilla. Anteriorly, the lamina horizontalis bears a ventral gutter that slopes upward. The processus palatinus is not preserved, but one specimen (MCM 68, Fig. 10C–D) shows the lamina horizontalis beginning to expand dorsally; this may represent the anterior limit of the processus palatinus. In the posterior region, the labial groove slopes gently, corresponding to the area on the lingual surface between the crista dentalis and the lamina horizontalis. The latter is shelf-like in cross-section, projecting twice as far as its width (Fig. 10E). No pronounced gutter is present ventrally or dorsally. The lamina is not parallel to the crista dentalis but slopes gently upward to a high abrupt posterior termination. The result is a large gap between it and the tops of the small cylindrical tooth pedicels.

*Atlas*.—Type 2 atlantes (MCM 81, 82) are broadly similar to those of Type 1 but are relatively shorter and wider, with an overall pentagonal shape (Fig. 5H). The anterior cotyles are separated by a small intervening surface that is perforated in both specimens by the remains of the notochordal canal, suggesting immaturity (Fig. 5F–G). The posterior face of the centrum contains a rounded cotyle that is perforated by a small notochordal canal (Fig. 5I).

*Sacral vertebra*.—MCM 85 (Fig. 6E–H) is a sacral vertebra of rather different morphology from those of Type 1. It is much more gracile than the adult Type 1 (even allowing for the smaller size), and the body of the bone is proportionally longer. Although of similar size to the juvenile Type 1, the posterior articular surface (Fig. 6E–F) is undivided and linear. It is slightly recessed and clearly held a cartilaginous (fibrocartilaginous) pad so that the sacrococcygeal joint was either a synchondrosis, the primitive condition (Trueb, 1973) seen in leiopelmatids, or an immature stage in the development of either monocondyly or sacro-urostyler fusion. Anteriorly, the centrum bears a large rounded cotyle, suggesting the last presacral vertebra was either procoelous or amphicoelous. The transverse processes angle posteriorly as in Type 1, but they differ in being dorsoventrally

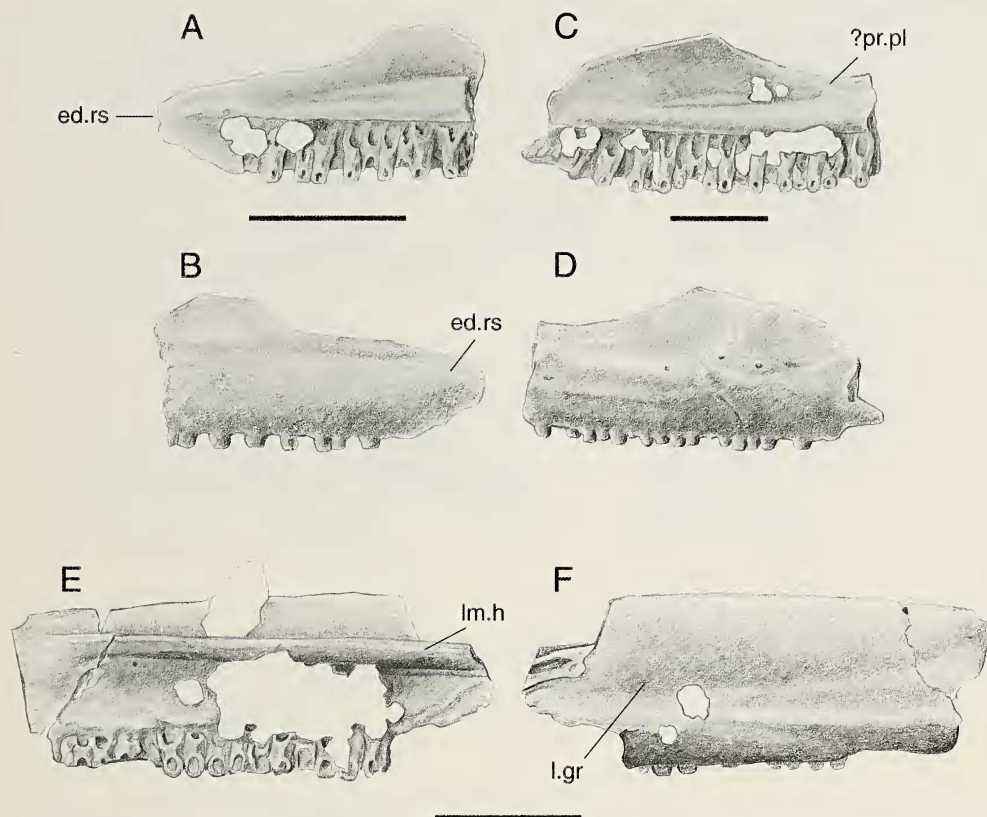


Fig. 10.—Anoual Type 2 anuran maxillae. A–B, MCM 67, anterior region of right bone, in A. Medial, and B. Lateral views. C–D, MCM 68, anterior region of right bone in C. Medial, and D. Lateral views. E–F, MCM 69, posterior region of right bone, in E. Medial, and F. Lateral views. Scale bars = 1 mm. White areas are matrix.

compressed with a slight distal flaring that suggests a gradual expansion towards the tips. The neural arch is more vaulted than that of Type 1, with a low median crest, relatively much smaller anterior zygapophyses, and no posterior pits for spinal connective tissues.

*Post-atlantal presacral vertebrae.*—Type 2 presacrals (e.g., MCM 77, 86, MCM 208–210) are characterized by several features: the centra are proportionally longer than those of Type 1; the neural arch pedicels are broad-based; the dorsal lamina is arched, anteriorly inclined, and has a moderately developed neural spine; and there is evidence of imbrication. The transverse processes are placed high on the neural arch and are more dorsoventrally compressed than those of Type 1 vertebrae. The majority of Type 2 vertebrae are amphicoelous and notochordal (e.g., MCM 77, Fig. 11A, B), with well-rounded anterior and posterior cotyles. However, the largest specimen (MCM 86, Fig. 11C–E), presumably an adult, is procoelous, with a fully developed posterior condyle. Nonetheless, the rounded cotyle and the central pit in the condyle suggest that this procoelously developed via a perichordal stage. As such, it does not fit Trueb's (1973) definition of procoely (derived from holochordy) but would fall within her category of anomocoelous, where centra are biconcave with a free intervertebral disc that adheres to the posterior end of the centrum without actually fusing to it, or fuses only at the adult stage. This is said to be a feature of terrestrial taxa (Trueb, 1973).

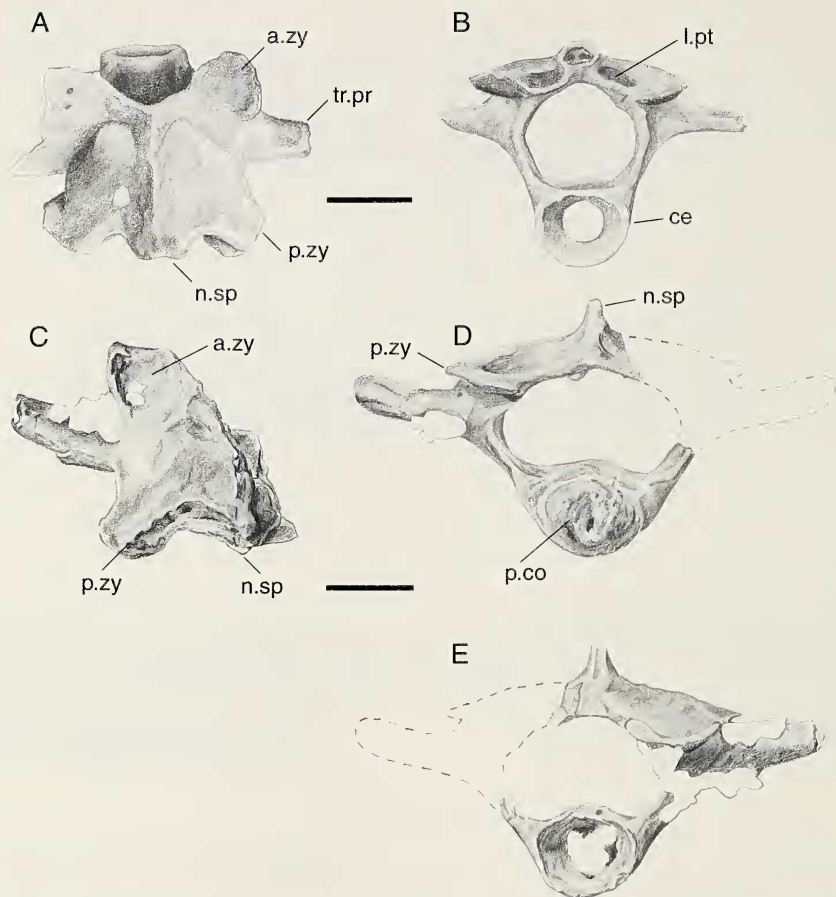


Fig. 11.—Anoual anuran presacrals, Type 2. A–B, MCM 77, immature Type 2 presacral, in A. Dorsal, and B. Posterior views. C–E, MCM 86, mature Type 2 presacral, in C. Dorsal, D. Posterior, and E. Anterior views. Scale bars = 1 mm. White areas are matrix.

*Scapula*.—Type 2 scapulae (e.g., MCM 95, Fig. 8B, E, F) have a longer, narrower blade than that of Type 1. This flares distally into the suprascapular attachment and has a distinct crest (anterior lamina) along the anterior margin. The edges are complete in MCM 95, and the blade was clearly narrower than that of Type 1. Proximally the bone is strongly bifurcate with a narrower cleft that is long and directed posterolaterally-anteromedially. The pars acromialis is mediolaterally thin, while the pars glenoidalis is ventrally extended and flared. The glenoid faces posterolaterally. MCM 96 (Fig. 8C) resembles the Type 2 scapulae in all respects, except for the much taller blade. Either it represents a third frog taxon in the assemblage or it is a variant (possibly pathological) of the Type 2 scapula. A tall blade like this is found in the living pelobatid *Scaphiopus* (Sánchez, 1998).

#### ADDITIONAL ANURAN SKELETAL ELEMENTS

*Introduction*.—A subset of skeletal elements shows no characters that would permit even tentative attribution to one or other frog taxon. These include the mandibles, urostyles, and



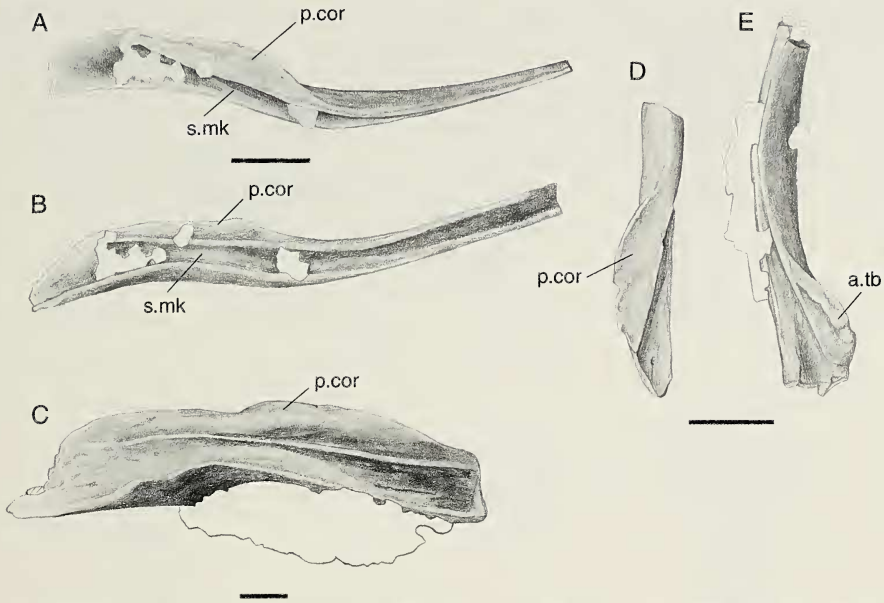


Fig. 12.—Anoual anuran angulosplenial. A–B, MCM 70, Type A right bone, in A. Dorsal, and B. Lateral views. C. MCM 71, Type A, right bone, in lateral view. D–E, comparison of D. MCM 72 (Type A, right bone) with E. MCM 74 (Type B, left bone) in dorsal view. Scale bars = 1 mm. White areas are matrix.

elements of the fore- and hindlimbs. In this section, where two morphotypes can be distinguished, they are designed Type A and Type B to preclude confusion with Types 1 and 2 as used above.

*Mandible.*—The anuran mandible consists of two bones (with or without ossified mentomeckelians)—the anterior dentary and the posterior angulosplenial. At Anoual, two types of angulosplenial are distinguished primarily by the anterior morphology of the processus coronoideus. Four specimens are confidently attributed to Type A (e.g., MCM 70–72; Fig. 12A–D) on the basis of a well-defined processus coronoideus with sharp lingual and labial edges. MCM 71 (Fig. 12C) is the largest specimen, presumably from an older individual. The processus coronoideus is slightly convex with a posterior gutter and a thin, raised, lingual edge. The small specimens possess an almost flat processus coronoideus, with the lingual edge slightly raised posteriorly while the labial edge is more prominent anteriorly. The lingual projection of the processus coronoideus is shelf-like and extends horizontally and medially.

A further four specimens (e.g., MCM 74, 75, 76, Fig. 12E) can be attributed to a second angulosplenial type. All preserve a small anterior part of the processus coronoideus (MCM 74, Fig. 12E) that is shallower than that of Type A (e.g., MCM 72, Fig. 12D), with a sharp labial edge and a rounded lingual edge bearing a weak anterior tubercle (a. tb, Fig. 12E). In addition, the process extends lingually at an oblique dorso-medial angle and its abutment with the rest of the bone is more gradual than that of Type A.

*Urostyle.*—The urostyle (or coccyx in Trueb, 1973) is formed by the fusion of post-sacral tail vertebrae. Five urostyles have been recovered, and they fall into three morphotypes—Type A (MCM 88, 89), Type B (MCM 90, 91), and a final specimen (MCM 92) that may be an aberrant form of Type A.

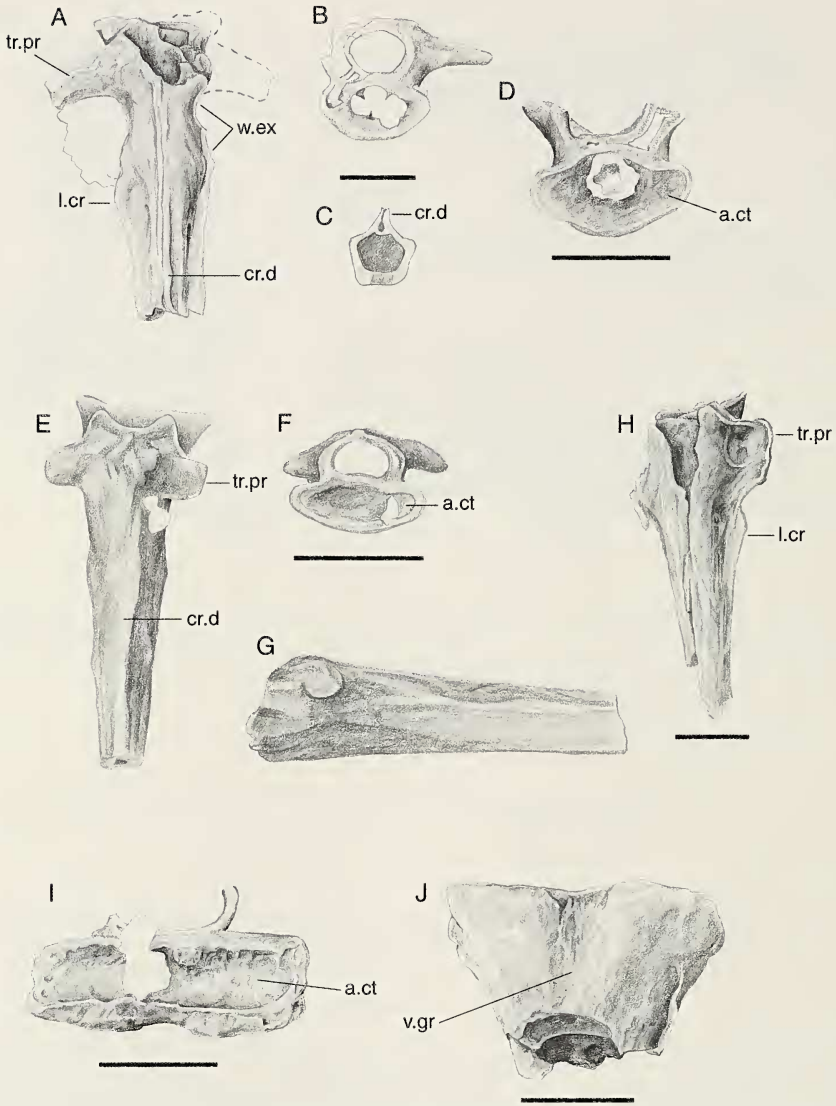


Fig. 13.—Anoual anuran urostyles. A–C, MCM 88, Type A urostyle, in A. Dorsal, B. Anterior, and C. Posterior cross-sectional views. D. MCM 89, Type A urostyle, anterior view. E–G, MCM 90, Type B urostyle, in E. Dorsal, F. Anterior, and G. Left lateral views. H. MCM 92, aberrant possible Type B urostyle, dorsal view. I, J, MCM 91, in I. Anterior, and J. Ventral views. Scale bars = 1 mm. White areas are matrix.

Type A urostyles are distinguished by a rounded, but laterally expanded anterior articular surface; prominent dorsal and lateral crests; a smooth ventral surface; and a pattern of waisting-expansion-constriction occurring posterior to the transverse processes (Fig. 13A–D). Only one specimen (MCM 88) preserves a transverse process and this shows a distinct posterior curvature. The upper surface is fairly flat while the ventral surface is rounded and anteriorly thickened, expanding medially to form a strong buttress. Both specimens (Fig. 13B, D) retain patent notochordal canals anteriorly and are therefore

probably immature. The dorsal crest is relatively well developed, but narrow, extending forward to at least the level of the transverse process.

Type B urostyles lack the distinctive features of Type A and have a relatively wider, more depressed anterior articular surface (Fig. 13F, I). Where preserved, the transverse processes are robust but short (Fig. 13E). There are no prominent lateral crests, while the dorsal crest begins weakly but becomes stronger and wider posteriorly. The most complete Type B urostyle is MCM 90 (Fig. 13E–G). Despite being very small, there is no trace of an anterior notochordal perforation. MCM 91 (Fig. 13J) is significantly larger and bears a subtle anteroventral groove.

MCM 92 (Fig. 13H) is damaged anteriorly, but the anterior surface does not appear conspicuously wide. The transverse process is thin, flat and broad-based. Posteriorly, it effectively grades into a prominent lateral crest, although a small notch separates the process from the crest on the right side. The degree of development of this crest appears to be asymmetrical on the two sides of the bone. In the presence of a dorsal crest, relatively narrow anterior articulation, longitudinal crest and waisting, MCM 92 resembles Type A urostyles, the main difference being the shape of the transverse process. Asymmetry in the form of the urostyle transverse process has been reported in recent taxa (e.g., discoglossids, ranids, Roček, 2000) and in the Jurassic *Notobatrachus* (Báez and Basso, 1996:143), but levels of inter- and intraspecific variation are not well studied in frogs.

*Forelimb elements.*—Most humeral specimens preserve only the distal end. MCM 97 is an exception (Fig. 14A–D) in retaining part of the proximal shaft. The crista ventralis is moderately developed while the crista paraventralis is present but more subtle (Fig. 14B). However, since the degree of development of these crests may be related to sexual dimorphism rather than phylogeny (Roček, 1994), this feature is probably not significant. The long axis of the bone is straight and the distal humeral condyle (eminentia capitata) lies centrally. The condyle is large relative to the overall distal width (roughly 72%), while the ulna epicondyle is small and the radial side unexpanded. Although the Anoual humeri show variation in features such as the position of the olecranon scar and the definition of the lateral border of the fossa cubitalis ventralis, these features can be size-related (e.g., Evans and Milner, 1993, MJ/SE personal observations).

The radioulna is represented by two specimens, of which MCM 98 is the better preserved (Fig. 14E). The olecranon process is well developed, suggesting a terrestrial frog with strong limbs.

*Hindlimb elements.*—MCM 99 appears to be the proximal head of an anuran femur (Fig. 15A). It is small but exhibits a pronounced crista femoris. Tibiofibulae are far more commonly represented and can be divided into two types based on cross-sectional shape and the development of the crista cruris (Fig. 15B–C). Type A tibiofibulae (e.g., MCM 100, Fig. 15B) seem to be relatively longer than Type B. They are generally rounded, with a circular cross-section centrally and a figure of eight cross-section proximally. The crista cruris is subtle and rounded. The tibia and fibula are parallel although centrally the fibula warps towards the tibia. Grooves marking the separation of the two bones are limited to the proximal and distal ends. Type B elements (e.g., MCM 73, Fig. 15C) differ in being squarer in cross-section with at least one well-defined corner. A pronounced crista cruris is present on the proximal part of the tibia. The tibia and fibula are parallel although the slightly smaller fibula narrows centrally. Allowing for the more fragmentary nature of Type B bones, the grooves separating the tibia and fibula appear more extensive than those of Type A.

MCM 76 is a partial tibiale-fibulare (not figured). The components are completely separated except at the distal tips, which are slightly expanded and fused.

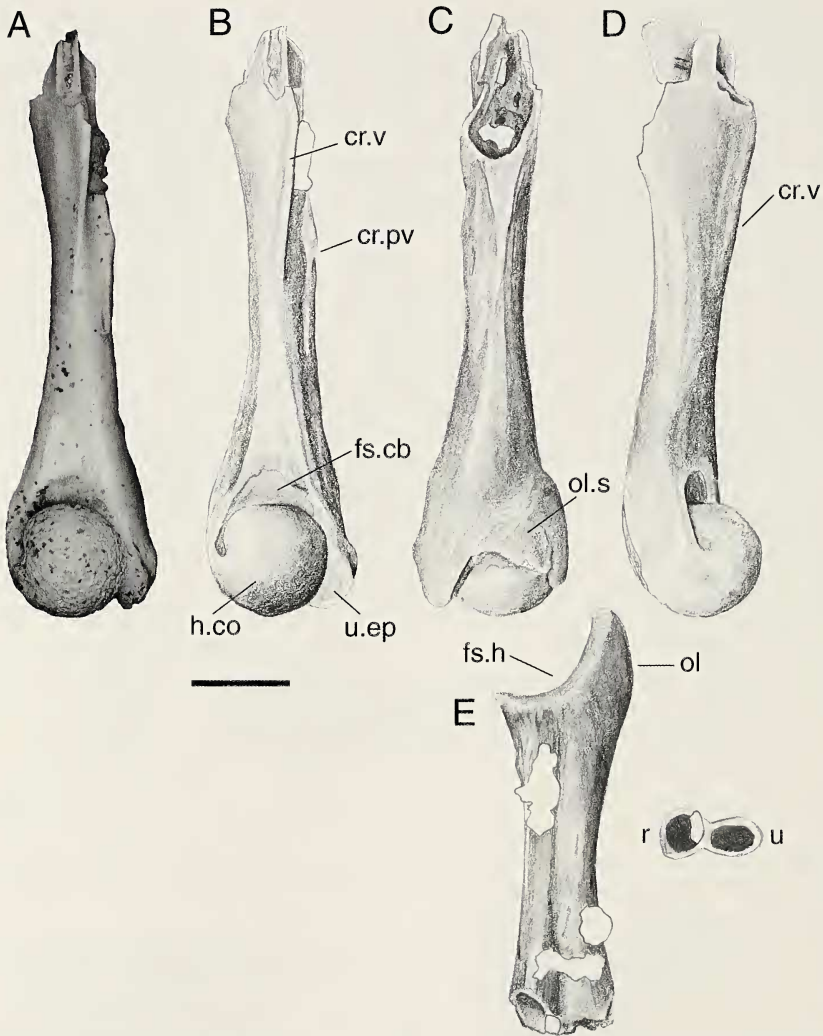


Fig. 14.—Anoual anuran forelimb elements. A–D, MCM 97, left humerus, in A. Scanning electron micrograph, ventral view, B. Ventral view, C. Dorsal view, D. Lateral view; E. MCM 98, radioulna. Scale bars = 1 mm. White areas are matrix.

## DISCUSSION

### *Comparison*

*Introduction.*—As far as we can determine, and allowing for two anomalous elements (the odd scapula, MCM 96, and urostyle, MCM 92), the Anoual remains are consistent with the presence of two distinct frog taxa in the deposit. Detailed cladistic analyses are obviously not possible with fragmentary material of this kind, but at least some of the skeletal elements preserved at Anoual are considered phylogenetically informative.

*Ilium.*—Ilium are the elements most commonly used in the diagnosis of anuran taxa from microvertebrate sites (Fig. 16). Widely used characters include the presence or absence of a dorsal crest; the shape of the blade and its relationship with the acetabular region; the

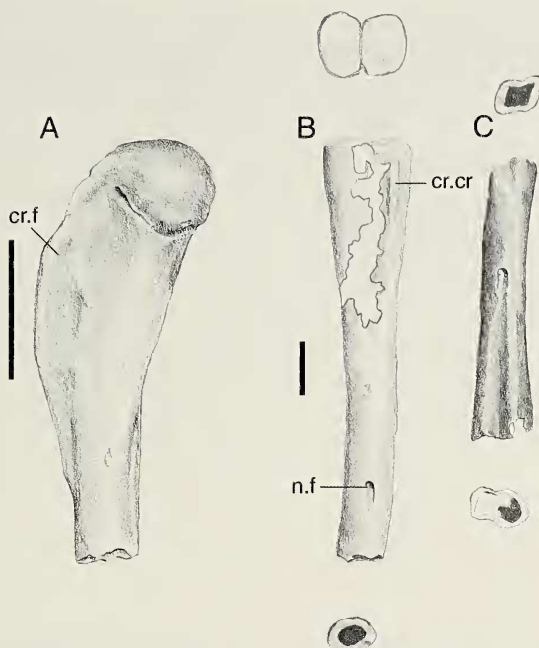


Fig. 15.—Anoual anuran hind limb elements. A. MCM 99, femoral head, lateral view. B. MCM 100, Type A tibiofibula, in dorsal view with proximal end and distal cross-section. C. MCM 73, Type B tibiofibula, dorsal view, with proximal and distal cross-sections. Scale bars = 1 mm. White areas are matrix.

presence, size and position of a tuber superior and/or dorsal prominence; the relative sizes of the partes ascendens and descendens; the degree of expansion, if any, of the acetabular rim; the presence or absence of a supraacetabular fossa; and the presence or absence, size, and position of any interiliac tuberosity (e.g., Sanchíz, 1998). On this basis, the Anoual ilia fall into two distinct morphotypes. Of these, one shows a close resemblance to the ilia of known Mesozoic discoglossids (particularly *Eodiscoglossus*, *Enneabatrachus*, *Paradisoglossus*, Fig. 16A–E) in the shape, size and position of the tuber superior, the shape of the iliac blade and its continuity with the acetabular region (no marked waisting), and a well-developed pars ascendens (Roček, 1994). As discussed above (Systematic Paleontology), the greatest similarity is with the Late Jurassic *Enneabatrachus hechti* from the Morrison Formation of the USA (Fig. 16A–B), although the Anoual forms differ in the presence of a weak interiliac tubercle, a less prominent tuber superior, and a less expanded ventral acetabular rim.

The second frog, *Aygroua*, has an ilium that is distinctive but not obviously attributable to a particular anuran clade. It differs from the ilium of most discoglossids in the shape of the blade, the presence of a dorsal prominence rather than a clear ovoid tuber superior, the relatively undeveloped pars ascendens, and the presence of a strong interiliac tuberosity. A strong, buttressed, interiliac tuberosity of this kind is found in pipimorph frogs (palaeobatrachids, pipids, e.g., Fig. 16F–H), and the flaring of the acetabular rim and the development of a dorsal prominence would be consistent with at least some of these groups (e.g., palaeobatrachids), as would the narrowing of the shaft immediately distal to the acetabulum (crests excepted) and the relatively low interiliac angle (Sanchíz and Roček, 1996; Trueb, 1996). The *Aygroua* ilium differs from that of living and fossil

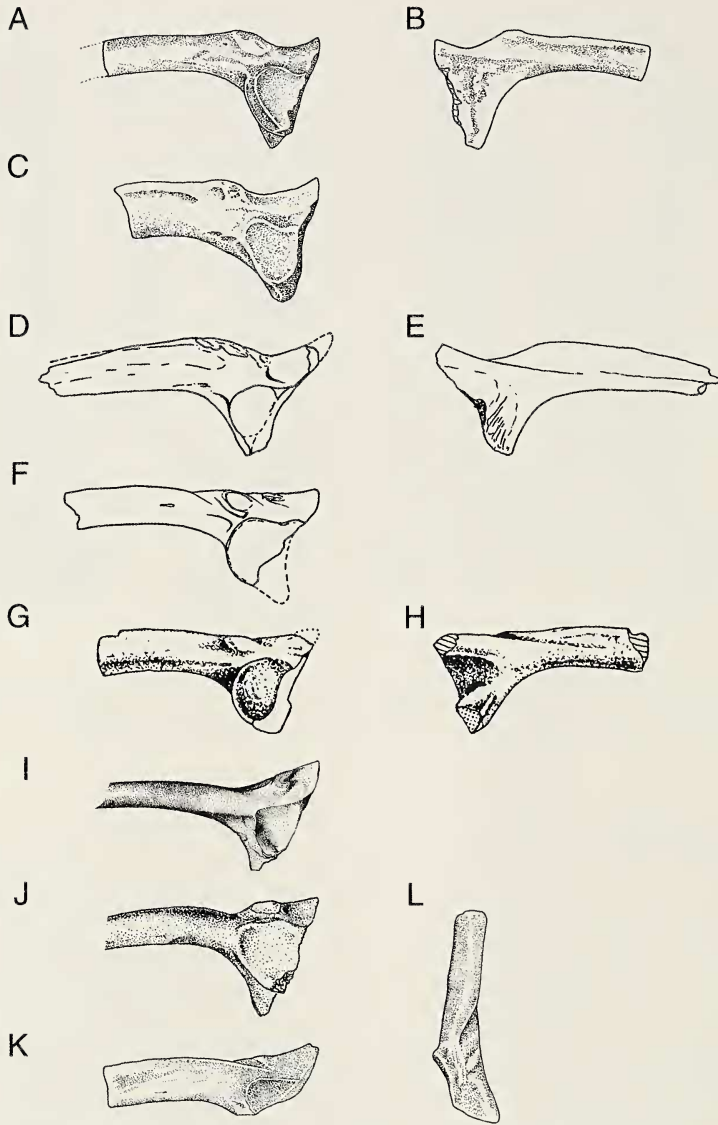


Fig. 16.—Comparison of iliac form in Anura. A–B, *Enneabatrachus hechti*, Upper Jurassic, North America, Discoglossidae, in A. Lateral, and B. Medial views. C, *Eodiscoglossus oxoniensis*, Discoglossidae, Middle Jurassic, England, lateral view. D–E, *Paradiscoglossus americanus*, Upper Cretaceous, North America, Discoglossidae, in D. Lateral, and E. Medial views. F, *Palaeobatrachus occidentalis*, Upper Cretaceous, North America, Palaeobatrachidae, in lateral view. G–H, *Pliobatrachus langhae*, Pleistocene, Romania, Palaeobatrachidae, in G. Lateral, and H. Medial views. I, *Scaphiopus alexanderi*, Miocene, North America, Pelobatidae, lateral view. J, *Tephrodytes brassicarvalis*, Oligocene, North America, Pelodytidae, lateral view. K–L, Pelobatoidea indet., Upper Jurassic, North America, in K. Lateral, and L. Posterior views. Figures not to scale. C, G–H, and K–L, have been reversed from the originals to aid comparison. (A–B, K–L, from Evans and Milner, 1993; C, from Evans et al., 1990; D–E, F, from Estes and Sanchíz, 1982b; G–H, from Sanchíz and Mlynarski, 1979; I, from Zweifel, 1956; J, from Henrici, 1994)

pelobatoids (Fig. 16I–L), however, in lacking the distinctive dorsal spiral groove (Evans and Milner, 1993; Henrici, 1994: seen most clearly in Fig. 16K–L). It further differs from that of living pipids in lacking the coossification of the pubis and ischium (although the juvenile condition of this has not been described) and in the possession of a rounded rather than elongate acetabulum (Trueb, 1996).

*Jaw elements.*—Most frogs have an abutting contact between the premaxilla and the maxilla, the two being held mostly by soft tissue, but pipimorphs (pipids and palaeobatrachids) share a derived condition (Trueb, 1973, 1993; Henrici, 1994, 1998*b*) whereby an edentulous process of the maxilla fits into a recess in the premaxilla. A similar condition occurs in some megophryine pelobatids (e.g., *Brachytarsophrys*, AMNH 23969; some species of *Megophrys*: *M. boettgeri*, AMNH 30361, and *M. lateralis*, AMNH 23549, but not *M. kuatunensis*, AMNH 30247: SE personal observation). Of the Anoual elements, the Type 1 maxilla and premaxilla show no evidence of a specialised articulation. They would be consistent with an attribution to the discoglossid or to any non-pipimorph frog. This conclusion is supported by the strong posterolingual process on the lamina horizontalis of the maxilla, a feature closely resembling that of the Tertiary genus *Latonia* (Roček, 1994). The Type 2 premaxilla, however, has a recess that matches the edentulous rostral part of the Type 2 maxilla. This configuration is not found in discoglossids and therefore the Type 2 elements may belong to *Aygroa*. Crown-group pipids are either edentate or have monocuspid acrodont teeth in which the pedicel has been lost (Trueb, 1996). Palaeobatrachids show the latter condition, while crown-group rhinophrynids are recorded as edentate (Trueb, 1973). However, the most basal rhinophrynid (*Rhadinosteus*, Henrici, 1998) retains bicuspid, pedicellate teeth, as does the Early Cretaceous pipimorph (contra pipid, Nevo 1968) *Thoraciliacus* (Trueb, 1999). The *Aygroa* maxilla and premaxilla therefore show a combination of character states consistent with those of a basal pipimorph.

*Atlas.*—Lynch (1971) described three atlantal types of which his ‘type II’ is generally thought to be the most primitive (e.g., Trueb, 1973), as it is found in archaic families (discoglossids, pelobatoids, rhinophrynids) and in the more primitive members of some neobatrachian lineages (e.g., ranids, bufonids, leptodactylids, Trueb, 1973). At Anoual, both atlantal morphotypes fit into this category, although the cotyles are more robust, rounded, and ventrally placed than those of most living anurans. The Anoual atlantes differ from one another in basic proportions (longer and narrower in Type 1) and the form of the posterior cotyle (wide and imperforate in Type 1). The Type 1 atlas is broadly similar to that of the discoglossids *Eodiscoglossus oxoniensis* (Middle Jurassic, Britain, Evans et al., 1990) and *E. santonjae* (Early Cretaceous, Spain, Estes and Sánchez, 1982*b*), although the cotyles are more circular (Evans et al., 1990). The imperforate posterior cotyle suggests opisthocoely in successive vertebrae—a feature that would be consistent with attribution to discoglossids (see below). On this basis, Type 2 atlantes should be attributable to *Aygroa*, but show no features that specify their placement into one of the higher clades. The retention of a notochordal perforation in the posterior cotyle could be a primitive feature, or an immature configuration in a perichordal genus trending to either procoely (anomocoely) or ‘functional opisthocoely’ (sensu Estes, 1975) (as seen, for example, in juveniles of *Megophrys*, SE personal observation).

The atlas is discrete in all anurans except most crown-group pipimorphs, where it tends to fuse with the first post-atlantal vertebra. This occurs in known palaeobatrachids and in derived pipids (Trueb, 1996), and in many (but not all) specimens of the early (Early Cretaceous, Barremian) pipimorph *Thoraciliacus* (Trueb, 1999).

*Post-atlantal presacral vertebrae.*—The vertebral characters most frequently used in discussions of relationships amongst anurans are centrum type, central articulation, and

neural arch imbrication (e.g., Trueb, 1973). Griffiths (1963) recognized three developmental patterns for the vertebral centra—ectochordal, stegochordal, and holochordal. Ectochordy (today more often referred to as perichordy, e.g. Duellman and Trueb, 1986), in which the centrum develops as a cylinder around a central notochord, appears to be the primitive condition, but may also be the developmental condition from which the other types arise (Mookerjee, 1931). In stegochordy and holochordy, the centra are solid (depressed in stegochordy and rounded in holochordy). Basal living frogs (*Ascaphus*, *Leiopelma*), and early fossil taxa such as *Prosalirus*, *Vieraella* and *Notobatrachus*, have perichordal vertebrae (Trueb, 1973; Báez and Basso, 1996; Shubin and Jenkins, 1995), and this was clearly the primitive condition. However, perichordy is also present in rhinophrynids (Trueb, 1996; Henrici, 1998b), in the early pipoid *Thoraciliacus* (Nevo, 1968; Trueb, 1999), and in *Eodiscoglossus* (Estes and Sanchíz, 1982a; Evans and Milner, 1993), although discoglossids and pipoids are generally characterized as stegochordal (Trueb, 1973). Whether this perichordy persists as a primitive feature or has been re-developed secondarily through pedomorphosis (Green and Cannatella, 1993) is unclear, but it shows that the presence of perichordy must be treated carefully in phylogenetic discussions.

Both Anoual vertebral types are amphicoelous and notochordal, suggesting perichordal development. This is problematic with respect to Type 1 centra since living discoglossids show epichordal (stegochordal) development (Griffiths, 1963; Púgener and Maglia, 1997), and this should not involve a perichordal stage. However, Type 1 presacral centra are closely similar to isolated centra attributed to the Jurassic-Cretaceous genus *Eodiscoglossus*, both in their overall morphology and the slight dorso-ventral compression (Estes and Sanchíz, 1982a; SE personal observation). Either *Eodiscoglossus* is not a discoglossid (see discussion below of discoglossid relationships), or the patterns of vertebral development were not as clear-cut in the early stages of anuran evolution. Type 1 specimen MCM 207 (Fig. 7G-I) clearly shows that one of the Anoual frogs had opisthocoelous vertebrae with a basically perichordal pattern of development. Type 2 centra are more cylindrical and most closely resemble those of the Jurassic rhinophrynid *Rhadinosteus* (Henrici, 1998b; SE personal observation), the extant *Rhinophrynus dorsalis* (SE personal observation), and juveniles of some pelobatoids (e.g., *Megophrys monticola*, AMNH 24786).

With respect to the articulations between centra, amphicoely is recognized as the primitive anuran condition (e.g., *Triadobatrachus*, *Czatkobatrachus*, ascaphids, presacrals of *Eodiscoglossus oxoniensis*, SE personal observation) but can also occur in juveniles of other groups. Opisthocoely is found in most discoglossids, in basal pipimorphs such as *Thoraciliacus* (Trueb, 1999), and in living pipids and rhinophrynids; procoely is known in palaeobatrachids, some pelobatoids, and advanced (neobatrachian) frogs. Thus although the opisthocoelous/amphicoelous Type 1 Anoual vertebrae could belong to either the discoglossid or, potentially, *Aygroa*, the procoelous/amphicoelous Type 2 vertebrae cannot belong to the discoglossid and are more parsimoniously attributable to *Aygroa*. Trueb (1973) restricted true procoely to vertebrae having holochordal (neobatrachians and some pelobatids), rather than stegochordal or perichordal centra (palaeobatrachids, pelodytids). In pelobatoids (e.g., *Megophrys*, SE personal observation), but also rhinophrynids, the intervertebral disc remains unfused to the centrum for at least part of the life history (Trueb, 1973), thus the presacrals are either amphicoelous throughout life, or amphicoelous in the juvenile and procoelous or opisthocoelous in the adult (anomocoelous, Trueb, 1973). It seems likely that a cylindrical perichordal vertebral centrum is primitive for mesobatrachians, and therefore also basal pipoids (Trueb, 1996), with the intercentral discs attaching either to the front or to the back of adjacent centra. In their



combination of perichordy, immature amphicoely, and adult procoely, the Type 2 vertebrae appear most consistent with attribution to either a primitive pelobatoid or a primitive palaeobatrachid (assuming the basal pipimorph condition to be perichordy).

Both Anoual vertebral types have weakly imbricating neural arch laminae—a condition that is widespread in basal frogs (discoglossids, some pipoids, some pelobatoids including pelobatines and rhinophrynids) and a smaller number of neobatrachians (e.g., dendrobatids, microhylids, Trueb, 1973). The presence of fused ribs on the transverse process of MCM 78 would be consistent with either a discoglossid or a primitive mesobatrachian (Trueb, 1973), although the shape of the process matches that of the Type 1 (?discoglossid) vertebrae.

*Sacral vertebrae*.—Only two phylogenetically useful characters have been described for the sacral vertebra—the shape of the transverse processes and the nature of the sacro-urostylar articulation (Emerson, 1979, 1982).

Sacral transverse processes are described as expanded (some basal frogs, many neobatrachians), very expanded (particularly pipids and some pelobatoids) or cylindrical (principally ranids, but also some fossil discoglossids). None of the Anoual sacra have complete processes, but those of Type 1 appear stout and cylindrical (similar to those in described discoglossids such as *Wealdenbatrachus*, *Eodiscoglossus santonjae*, Sanchíz, 1998) while those of Type 2 are dorso-ventrally flattened and show a slight distal expansion (but less so than in *Thoraciliacus*).

In *Ascaphus* and *Leiopelma*, a pad of fibrocartilage connects the sacrum and urostyle, forming a synchondrosis. Since this is similar to the structure of a typical intervertebral joint, it is probably the primitive condition. A bicondylar joint develops in a majority of crownward anuran lineages including discoglossids, rhinophrynids, and myobatrachids, but the bones fuse in pipids, and either fuse or develop a monocondylar joint in pelobatoids. In *Thoraciliacus*, the articulation is monocondylar (Trueb, 1999). On this basis, the bicondylar Anoual Type 1 sacrum could belong to one of a number of anuran families (including discoglossids), but would be incompatible with most pipids or pelobatoids (although exceptions occur); its anterior condyle, however, is most suggestive of a discoglossid since it implies the bicondylar state combined with opisthocoely. In fact, the short, wide Anoual Type 1 sacral, with its large zygapophyses and broad transverse processes closely resembles that figured for *Wealdenbatrachus* (Early Cretaceous, Spain, Fey, 1988), allowing for the more posteriorly oriented processes of that genus. Although rhinophrynids are also 'functionally opisthocoelous' (Estes, 1975), the intervertebral disc does not fuse to the vertebral body and macerated vertebrae appear amphicoelous (Henrici, 1998*b*, SE personal observation).

The Type 2 sacrum is different. The well-defined pitted posterior recess probably held a pad of fibrocartilage, suggesting either a primitive synchondrosis or a step towards fusion/monocondyly. Without a detailed account of the developmental stages in fusion and monocondyly for various groups, it is difficult to judge.

Palaeobatrachid frogs show a tendency (*Palaeobatrachus*, *Pliobatrachus*) towards fusion of the sacral vertebra with one or more of the preceding presacrals to form a synsacrum (Špinar, 1972). In contrast, many pipoids (Trueb, 1996) and pelobatoids (e.g., *Pelobates*, *Megophrys*, SE personal observation) fuse the sacrum and urostyle, while incorporating one or more postsacrals (as shown by the presence of distinct spinal nerve foramina). There is no evidence that fusions of either type occurred amongst the Anoual frog material.

*Urostyles*.—Apart from the sacro-urostylar joint, the presence or absence of transverse processes is the only consistent urostylar character to be discussed. Transverse processes are retained in several basal frog lineages—*Ascaphus*, *Leiopelma*, discoglossids and

pelobatids, with the condition in pipids, leptodactylids, and bufonids considered variable (Trueb, 1973). Transverse processes are absent in the Jurassic *Notobatrachus* (Baéz and Basso, 1996), but present in the basal pipimorph *Thoraciliacus* (Trueb, 1999). The retention of transverse processes on all Anoual urostyles supports their attribution to basal or mesobatrachian frog lineages.

*Pectoral girdle and forelimb.*—No consistently applicable humeral or radioulna characters have been identified, except for the derived enlargement of the distal humeral condyle (greater than 60% of the overall distal humeral width, Báez and Basso, 1996; Gao and Wang, 2001). There are, however, features of the scapula that may be useful in discussion. A short stocky scapula is found in most primitive anurans and pipimorphs (Trueb, 1973). The scapula of *Rhinophrynus* and pelobatoids is 2–3 times longer than wide. In pipids, the blade is short (but probably secondarily so, Cannatella and Trueb, 1988), and shows fusion of the clavicle to the scapula. The scapula is proximally cleft in most lineages (except *Ascaphus*, some *Leiopelma*, most pipids), although the depth and orientation of the cleft varies. A direct medio-lateral cleft appears to be primitive (e.g., *Czatkobatrachus*, *Eodiscoglossus oxoniensis*, *Prosalirus*), an oblique cleft—anterolateral to posteromedial—is more derived (e.g., *Rana*) (Borsuk-Bialynicka and Evans, 2002).

The two Anoual scapula morphotypes differ principally in their relative lengths, in the orientation of the scapular cleft, and in the presence (Type 2) of a crest or lamina along the anterior margin of the scapula (a pelobatoid character, Henrici, 1994, although in these taxa the crest typically runs the entire length of the scapula blade). The short, broad Type 1 scapula would be consistent with most basal frogs except *Ascaphus* and the derived pipids that lack a scapular cleft (*Leiopelma* shows variation, Sanchíz, 1998); the mediolateral orientation of the cleft suggests a basal rather than a derived frog. This type would therefore be consistent with attribution to a discoglossid and broadly resembles the scapula described for *Eodiscoglossus oxoniensis* (Evans et al., 1990). If this is correct, then the Type 2 scapula should belong to *Aygroa*. It is longer and relatively narrower, with an oblique cleft and an anterior crest. This scapula type most closely resembles that of pelobatoid frogs and rhinophrynids (Henrici, 1994; SE personal observation), although in the latter group, the scapular cleft is medio-laterally oriented rather than oblique. The anterior crest is variable in its degree of development. In pipimorphs, including *Thoraciliacus* (Trueb, 1999), the scapula is shorter and also wider along its suprascapular margin. The scapula remains cleft in *Thoraciliacus*, but loses the cleft in the extant genus *Pipa*, supposedly in relation to its strong aquatic specializations (Trueb, 1973, 1996). The morphology of the Type 2 scapula is thus consistent with attribution to a mesobatrachian frog, but the combination of character states is problematic.

#### CONCLUSIONS

*Introduction.*—The fragmentary frog remains from Anoual demonstrate the presence of two distinct taxa. The presence of opisthocoelous and procoelous vertebrae respectively place these frogs above the level of *Ascaphus* and *Leiopelma* (and thus also of *Vieraella*, *Notobatrachus*, and *Prosalirus*), while the combination of perichordal vertebrae and transverse processes on the urostyles make neobatrachian status less plausible. Of the two Anoual taxa, one shows affinity to discoglossids, while the other appears to be a mesobatrachian.

*Enneabatrachus.*—The attributed ilia are closely similar to those of early discoglossids, particularly the Jurassic *Eodiscoglossus oxoniensis* (Evans et al., 1990) and *Enneabatrachus hechti* (Evans and Milner, 1993). They are tentatively referred to *Enneabatrachus*. One group (Type 1) of supplementary elements is also consistent with this interpretation.

If correctly attributed, these elements suggest that the Anoual discoglossid had opistho-coelous vertebrae (but with either primitive or paedomorphic perichordal development), with weakly imbricate vertebral neural arches, fused ribs on at least some vertebrae, a bicondylar sacrum, and a short, broad, mediolaterally cleft scapula.

The monophyly of Discoglossidae remains contested (e.g., Ford and Cannatella, 1993; but see Clarke, 1988; Sanchíz, 1998; Gao and Wang, 2001). Several discrete lineages have been recognized: Alytinae (the living *Alytes*); Bombinatorinae (the living *Bombina* and *Barbourula*); and Discoglossinae (the living *Discoglossus* and a series of referred fossil taxa including *Eodiscoglossus*, *Latonia*, *Paradiscoglossus*, and *Wealdenbatrachus*); and, less certainly, Gobiatinae (Late Cretaceous frogs from Asia) (Sanchíz and Růček, 1996; Sanchíz, 1998). Ford and Cannatella (1993) split the living taxa between the Bombinatoridae and Discoglossidae, but place *Eodiscoglossus* in an unresolved trichotomy with Bombinatoridae and the ancestry of all other frogs (their Discoglossanura). Gao and Wang (2001), by contrast, recovered a clade comprised of *Eodiscoglossus*, *Bombina*, and *Barbourula* in combination with their Early Cretaceous *Callobatrachus* (Wang and Gao, 1999). This clade formed the sister group of *Discoglossus* + *Alytes*, within a monophyletic Discoglossidae. The Jurassic *Ennebatrachus* and the Late Cretaceous *Scotiophryne* are of uncertain position (Sanchíz, 1998), although *Ennebatrachus*, at least, has a general resemblance to *Eodiscoglossus oxoniensis*.

*Aygroa*.—The second frog has an ilium that is sufficiently distinctive to permit the recognition of a new genus. Its phylogenetic position is more problematic. The ilium of *Aygroa* is consistent with attribution to a pipimorph frog (sensu Ford and Cannatella, 1993) in several features including: the large interiliac synchondrosis and relatively narrow interiliac angle; the narrow iliac shaft; and the absence of a dorsal tuberosity, but development of a crest-like dorsal prominence. It differs from the ilium of all pelobatoids in the absence of the characteristic spiral groove (Evans and Milner, 1993; Henrici, 1994) and in the development of the interiliac tuberosity (also absent in rhinophrynids). Pipimorph attribution would also be supported by the strong maxillary/premaxillary overlap (with a well-developed edentulous anterior maxillary process), although this feature can occur, independently, in megophryine pelobatids. The vertebrae have a juvenile morphology consistent with that of mesobatrachian frogs (rounded perichordal centrum, amphicoely in juvenile) and an adult morphology (procoely) found in some pelobatoids, in palaeobatrachid pipimorphs, and in neobatrachians. The scapula, if correctly attributed, most closely resembles that of pelobatoids (long blade, anterior lamina present, Henrici, 1994) and, to a lesser degree, rhinophrynids.

One further genus merits brief consideration. Until recently, procoely was regarded as a derived condition within crown-group Anura. Gao and Wang (2001) have described a plausibly procoelous frog (*Mesophryne*) from the Lower Cretaceous of China. Their cladistic analysis places this new genus on the anuran stem, raising the possibility, as yet unconfirmed, that procoely arose repeatedly at different stages of anuran evolution. Nonetheless, *Mesophryne* differs substantially from *Aygroa* in details of the pelvic morphology (see above) and premaxillary-maxillary contact.

In summary, *Aygroa* shows two out of six characters listed by Henrici (1998b) as characterizing pipimorphs, namely the interiliac tuberosity and the maxillary/premaxillary overlap. A further three characters are unknown in *Aygroa* (long metapodials, ossified pubis, ribs present), while the sixth (teeth conical) is absent in *Aygroa* (pedicellate and bicuspid), but also in *Thoraciliacus* (pedicellate and bicuspid), classified as a basal pipimorph by Trueb (1999). *Thoraciliacus* shares the maxillary/premaxillary overlap with *Aygroa* and pipimorphs (although it is difficult to determine the degree of this overlap in *Thoraciliacus*). The two fossil taxa also resemble one another in retaining rounded

perichordal centra, at least in the juvenile, but differ in that while *Aygroa* develops towards procoely, *Thoraciliacus* becomes opisthocoelous. They also differ markedly in scapular morphology and in the shape of the sacral transverse processes (more greatly flared distally in *Thoraciliacus*).

Allowing for the fragmentary nature of the Anoual material, and the necessarily tentative nature of element attribution, the existing evidence suggests that *Aygroa* is a mesobatrachian frog allied either to basal pelobatoids, to basal pipimorphs, or to basal palaeobatrachids. If a basal pelobatoid, *Aygroa* would represent a stage either prior to the development of the dorsal spiral groove on the ilium or a reversal of this state, while the premaxillary/maxillary overlap and strong interiliac tuberosity would have been acquired independently (as in *Megophrys*). Interpretation as a basal pipimorph would be consistent with the overlapping premaxillary/maxillary contact and several pelvic features (see above), and would be unaffected by the retention of pedicellate, bicuspid teeth, but it would require that perichordy or anomocoely is primitive to the clade (a reasonable assumption given the condition in *Thoraciliacus*), with procoely or opisthocoely both possible. Attribution to a basal palaeobatrachid would be consistent with procoely, but would require that loss of pedicellularity had evolved independently in both pipids and palaeobatrachids, and that *Aygroa* represents a stage prior to the fusion of V1 and V2, fusion of the sacrum and posterior presacrals, and reduction of the maxillary dentition (12–16 teeth in palaeobatrachids, Sanchíz, 1998). Loss of the bicondylar sacrum in *Aygroa* would be secondary.

Currently, the oldest recorded mesobatrachians are from the Upper Jurassic Morrison Formation of the U.S.A., with an indeterminate pelobatoid (Evans and Milner, 1993) and a pipoid (a possible basal rhinophrynid, Henrici, 1998*b*). Pipoids have also been recorded from the Lower Cretaceous of Israel (*Cordicephalus* and *Thoraciliacus*, Nevo, 1968; Trueb, 1999), while palaeobatrachids are first recorded with confidence from the Upper Cretaceous (Sanchíz and Roček, 1996; Sanchíz, 1998). The basal Cretaceous *Neusibatrachus* (Montsech, Spain) was referred to the Palaeobatrachidae by Seiffert (1972) and by Estes and Reig (1973). Sanchíz (1998) synonymised the taxon with *Eodiscoglossus santonjae* from the same locality, although Roček (2000) has queried this. The earliest confidently recorded neobatrachians are leptodactylids from the Late Cretaceous of Brazil (Báez and Peri, 1989).

#### *Palaeobiogeographic implications*

To date, living and extinct discoglossids, pelobatoids, rhinophrynids, and palaeobatrachids are limited to northern continents or to regions that have clearly been colonized from the north (e.g., India). Pipids may fill the niche of pelobatoids and palaeobatrachids in Southern continents (Gondwana, e.g., Báez, 1981, 1996), while neobatrachian frogs may also have evolved and radiated from the south (Duellman and Trueb, 1986). Although albumin studies have suggested an origin for pipoids at about 130 Ma (Bisbee et al., 1977), the evidence from the fossil record would place it earlier than this. Since rhinophrynids (Henrici, 1998*b*) and, apparently, pelobatoids (Evans and Milner, 1993) are recognized from at least the Late Jurassic (Kimmeridgian, ca. 145 Ma), their ancestors must have separated during or before the Middle Jurassic (ca. 160 Ma). The breakup of Pangea was occurring about this time (Bajocian–Callovian, ca. 170–160 Ma, Smith et al., 1994; Dercourt et al., 2000), and it is plausible that this divided the ancestral pipimorph stock, with pipids developing in Gondwana (e.g., Báez et al., 2000) and palaeobatrachids in Laurasia (Sanchíz and Roček, 1996); pelobatoids remained in Laurasia, and rhinophrynids may have evolved in North America (Duellman and Trueb, 1986).

Similar arguments cannot be applied to discoglossids, monophyletic or not, since they were apparently in existence by the Bathonian (Evans et al., 1990). However, following a theory proposed by Hallam (1975), Růček (2000) has suggested that an arid equatorial belt might have restricted the spread of discoglossids to southern continents in the Jurassic. This would not be contradicted by the presence of the group in northwest Africa, a region to the north of the arid belt.

#### ACKNOWLEDGMENTS

Our thanks to Amy Henrici (Carnegie Museum of Natural History, Pittsburgh) for discussions on pipoid frogs and access to material of modern and fossil rhinophrynids and pipids; to Dr. Linda Ford (American Museum of Natural History, New York), and Dr. Barry Clarke (The Natural History Museum, London), who provided access to comparative material of pelobatoids and discoglossids respectively; to Dr. Andrew Milner (Birkbeck, London) and Amy Henrici, who reviewed an earlier version of this manuscript; and to Bethsaida Baddouh, Department of African Languages and Literature, University of Wisconsin at Madison, who provided help with the Berber language. Jane Pendjiky (UCL) assisted in the preparation of the figures for publication.

#### LITERATURE CITED

- ASHER, R. J., AND D. KRAUSE. 1998. The first pre-Holocene (Cretaceous) record of Anura from Madagascar. *Journal of Vertebrate Paleontology*, 18:696–699.
- BÁEZ, A. M. 1981. Redescription and relationships of *Saltenia ibanezi*, a Late Cretaceous pipid frog from northwestern Argentina. *Ameghiniana*, 18:127–154.
- . 1996. The fossil record of the Pipidae. Pp. 329–347, in *The Biology of Xenopus* (R. C. Tinsley, and H. R. Kobel, eds). Clarendon Press, Oxford, United Kingdom.
- BÁEZ, A. M., AND N. G. BASSO. 1996. The earliest known frogs of the Jurassic of South America, Review and cladistic appraisal of their relationships. *Münchener Geowissenschaftliche Abhandlungen*, A 30:131–158.
- BÁEZ, A. M., AND S. PERI. 1989. *Baurubatrachus pricei*, nov. gen. and sp., un Anuro del Cretacico superior de Minas Gerais, Brasil. *Anais Academia Brasileira Ciencias*, 61:447–458.
- BÁEZ, A. M., AND J. C. RAGE. 1998. Pipid frogs from the Upper Cretaceous of In Beceten, Niger. *Palaeontology*, 41:669–691.
- BÁEZ, A. M., L. TRUEB, AND J. O. CALVO. 2000. The earliest pipoid frog from South America: A new genus from the middle Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, 20:490–500.
- BISBEE, C. A., M. A. BAKER, A. C. WILSON, I. HADJI-AZIM, AND M. FISCHBERG. 1977. Albumin phylogeny for clawed toads (*Xenopus*). *Science*, 195:785–787.
- BORSUK-BIALYNICKA, M., AND S. E. EVANS. 2002. A scapulocoracoid of an early Triassic stem-frog from Poland. *Acta Palaeontologica Polonica*, 47:79–96.
- BRON, F. DE, E. BUFFETAUT, J. C. KOENINGUER, D. RUSSELL, P. TAQUET, C. VERGNAUD-GRAZZINI, AND S. WENZ. 1974. Le faune de vertébrés continentaux du gisement d'In Beceten (Sénonien du Niger). *Comptes Rendus de l'Académie des Sciences Paris*, D, 279:469–472.
- BROCHINSKI, A., AND D. SIGOGNEAU-RUSSELL. 1996. Remarkable lizard remains from the Lower Cretaceous of Anoual (Morocco). *Annales de Paléontologie*, 82:147–175.
- CANNATELLA, D. C., AND L. TRUEB. 1988. Evolution of the pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of the Linnean Society*, 94:1–38.
- CLARKE, B. T. 1988. Evolutionary relationships of the discoglossid frogs—osteological evidence. Unpublished Ph.D thesis, City of London Polytechnic.
- CONGLETON, J. D. 1988. Early Cretaceous vertebrate fossils from the Koum Basin, Northern Cameroon. *Journal of Vertebrate Paleontology*, 8:12A.
- DERCOURT, J., M. GAETANI, B. VRIELYNET, E. BARRIER, B. BIJU-DUVAL, M. F. BRUNET, J. P. CADET, S. CRASQUIN, AND M. SANDULESCU. 2000. Atlas Peri-Tethys Palaeogeographical maps. Peri-Tethys Programme, Paris.
- DUELLMAN, W. E. 1975. On the classification of frogs. *Occasional Papers*, Museum of Natural History, University of Kansas, 42:1–14.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of the Amphibians*. The Johns Hopkins University Press, Baltimore and London.
- DUFFIN, C. J., AND D. SIGOGNEAU-RUSSELL. 1993. Fossil shark teeth from the early Cretaceous of Anoual, Morocco. *Belgian Geological Survey, Professional Papers*, 264:175–190.
- EMERSON, S. B. 1979. The ilio-sacral articulation in frogs: form and function. *Biological Journal of the Linnean Society*, 11:153–168.
- . 1982. Frog postcranial morphology: Identification of a functional complex. *Copeia*, 3:603–613.

- ESTES, R. 1975. Lower vertebrates from the Fort Union Formation, Late Paleocene, Big Horn Basin, Wyoming. University of California, Publications of the Department of Geological Sciences, 49:365–385.
- . 1977. Relationships of the South African fossil frog *Eoxenopoides reuningi* (Anura, Pipidae). *Annals of the South African Museum*, 73:49–80.
- ESTES, R., AND O. A. REIG. 1973. The early fossil record of frogs: a review of the evidence. Pp. 11–63, in *Evolutionary Biology of the Anurans* (J. L. Vial, ed.). University of Missouri Press, Columbia.
- ESTES, R., AND B. SANCHÍZ. 1982a. Early Cretaceous lower vertebrates from Galve (Teruel), Spain. *Journal of Vertebrate Paleontology*, 2:21–39.
- . 1982b. New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek Formations. *Journal of Vertebrate Paleontology*, 2:9–20.
- EVANS, S. E., AND M. BORSUK-BIALYNICKA. 1998. A stem group frog from the early Triassic of Poland. *Acta Palaeontologica Polonica*, 43:573–580.
- EVANS, S. E., AND M. MANABE. 1998. Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleontological Research, Japan*, 2:275–278.
- EVANS, S. E., AND A. R. MILNER. 1993. Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. *Journal of Vertebrate Paleontology*, 13:24–30.
- EVANS, S. E., A. R. MILNER, AND F. MUSSETT. 1990. A discoglossid frog from the Middle Jurassic of England. *Palaeontology*, 33:299–311.
- EVANS, S. E., A. R. MILNER, AND C. WERNER. 1996. New salamander and caecilian material from the late Cretaceous of the Sudan. *Palaeontology*, 39:77–95.
- EVANS, S. E., AND D. SIGOGNEAU-RUSSELL. 1997. New sphenodontians (Diapsida: Lepidosauromorpha: Rhynchocephalia) from the Early Cretaceous of North Africa. *Journal of Vertebrate Paleontology*, 17:45–51.
- . 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. *Palaeontology*, 44:259–273.
- FEY, B. 1988. Die anurenfauna aus der unterkreide von Uña (Ostspanien). *Berliner Geowissenschaftliche Abhandlungen, Reihe A*, 103:1–125.
- FLYNN, J. L., AND M. BRUNET. 1989. Early Cretaceous vertebrates from Cameroon. *Journal of Vertebrate Paleontology*, 9(supplement no. 3):21A.
- FORD, L. S., AND D. C. CANNATELLA. 1993. The major clades of frogs. *Herpetological Monographs*, 7:94–117.
- GAO, K., AND Y. WANG. 2001. Mesozoic anurans from Liaoning province, China, and phylogenetic relationships of archaeobatrachian anuran clades. *Journal of Vertebrate Paleontology*, 21:460–476.
- GREEN, D. M., AND D. C. CANNATELLA. 1993. Phylogenetic significance of the amphicoelous frogs, Ascaphidae and Leiopelmatidae. *Ethology, Ecology, Evolution*, 5:233–245.
- GRIFFITHS, I. 1963. The phylogeny of the Salientia. *Biological Reviews*, 38:241–292.
- HALLAM, A. 1985. A review of Mesozoic climates. *Journal of the Geological Society, London*, 142:433–445.
- HAUGHTON, S. H. 1931. On a collection of fossil frogs from the clays at Banke. *Transactions of the Royal Society of South Africa*, 19:233–249.
- HAY, J. M., I. RUVINSKY, S. B. BLAIR HEDGES, AND L. R. MAXSON. 1995. Phylogenetic relationships of the amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Molecular Biology and Evolution*, 12:928–937.
- HECHT, M. K. 1970. The morphology of *Eodiscoglossus*, a complete Jurassic frog. *American Museum Novitates*, 2424:1–17.
- HEDGES, S. B., AND L. R. MAXSON. 1993. A molecular perspective on lissamphibian phylogeny. *Herpetological Monographs*, 7:56–63.
- HENRICI, A. C. 1994. *Tephrodytes brassicarvalis*, new genus and species (Anura: Pelodytidae), from the Arikarean Cabbage Patch Beds of Montana, USA and, Pelodytid-Pelobatid relationships. *Annals of the Carnegie Museum*, 63:155–183.
- . 1998a. New anurans from the Rainbow Park Microsite, Dinosaur National Monument, Utah. *Modern Geology*, 23:1–16.
- . 1998b. A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology*, 18:321–332.
- HILLIS, D. M., L. K. AMERMAN, M. T. DIXON, AND R. O. DE SÁ. 1993. Ribosomal DNA and the phylogeny of frogs. *Herpetological Monographs*, 7:118–131.
- JACOBS, L. L., D. A. WINKLER, Z. M. KAUFULU, AND W. R. DOWNS. 1990. The Dinosaur beds of Northern Malawi, Africa. *National Geographic Research*, 6:196–203.
- JENKINS, F. A., AND N. H. SHUBIN. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology*, 18:495–510.
- LAURENT, R. F. 1979. Esquisse d'une phylogenie des anoures. *Bulletin de la Societe zoologique de France*, 104:397–422.

- LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. University of Kansas Museum of Natural History, Miscellaneous Publications, 53:1–238.
- MOOKERJEE, H. K. 1931. On the development of the vertebral column in Anura. Philosophical Transactions of the Royal Society of London, B 219:165–196.
- NEVO, E. 1968. Pipid frogs from the Early Cretaceous of Israel and pipid evolution. Bulletin of the Museum of Comparative Zoology, 136:255–318.
- RAGE, J.-C., AND Z. ROČEK. 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. Palaeontographica, A206:1–16.
- REIG, O. 1961. Noticia sobre un Nuevo fósil del Jurásico de Santa Cruz (Patagonia). Ameghiniana, 2:73–78.
- RICHTER, A. 1994. Lacertilia aus der Unteren Kreide von Úna und Galve (Spanien) und Anoual (Marokko). Berliner geowissenschaftliche Abhandlungen, 14:1–147.
- ROČEK, Z. 1994. Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* V. Meyer, 1843. Geobios, 27:717–751.
- . 2000. Mesozoic anurans. Pp. 1295–1331, in Amphibian Biology, Vol. 4 (H. Heatwole, H. and R. L. Carroll, eds.). Surrey Beatty and Sons, Chipping Norton, Australia.
- PÜGENER, L. A., AND A. M. MAGLIA. 1997. Osteology and skeletal development of *Discoglossus sardus* (Anura: Discoglossidae). Journal of Morphology, 233:267–286.
- SANCHÉZ, B. 1998. Salientia. Pp. 1–276, in Encyclopedia of Palaeoherpetology (P. Wellnhofer, ed.). Verlag Dr. Friedrich Pfeil, München, Germany.
- SANCHÉZ, B., AND M. MLYNARSKI. 1979. Remarks on the fossil anurans from the Polish Neogene. Acta Zoologica Cracoviensia, 24:153–174.
- SANCHÉZ, B., AND Z. ROČEK. 1996. An overview of the anuran fossil record. Pp. 318–328, in The Biology of *Xenopus* (R. C. Tinsley and H. R. Kobel, eds.). Clarendon Press, Oxford, United Kingdom.
- SEIFFERT, J. 1972. Ein Vorläufer der Froschfamilien Palaeobatrachidae und Ranidae im Grenzbereich Jura-Kreide. Neues Jahrbuch der Mineralogie, Geologie, und Paläontologie, Monatshefte, 1972:120–131.
- SHUBIN, N. H., AND F. JENKINS. 1995. An Early Jurassic jumping frog. Nature, 377:49–52.
- SIGOGNEAU-RUSSELL, D. 1988. Découverte de mammifères dans le Mésozoïque moyen d'Afrique. Comptes Rendus de l'Académie des Sciences, II, 307:1045–1050.
- . 1991a. Découverte du premier mammifère tribosphenique du Mésozoïque africain. Comptes rendus hebdomadaires des séances de l'Académie des sciences, ser. D, sciences naturelles, Paris, 313:1635–1640.
- . 1991b. First evidence of Multituberculata (Mammalia) in the Mesozoic of Africa. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1991:119–125.
- . 1992. *Hypomylos phelizoni* nov. gen. nov. sp., une étape précoce de l'évolution de la molaire tribosphenique (Crétacé basal du Maroc). Geobios, 25:389–393.
- . 1995. Further data and reflexions on the tribosphenid mammals (Tribotheria) from the Early Cretaceous of Morocco. Bulletin du Muséum National d'Histoire naturelle, 16:291–312.
- SIGOGNEAU-RUSSELL, D., M. MONBARON, AND E. DE KAENEL. 1990. Nouvelles données sur le gisement à mammifères mésozoïques du Haut-Atlas Marocain. Geobios, 23:461–483.
- SIGOGNEAU-RUSSELL, D., S. E. EVANS, J. F. LEVINE, AND D. A. RUSSELL. 1998. The Early Cretaceous microvertebrate locality of Anoual, Morocco: A glimpse at the small vertebrate assemblages of Africa. In Lower and Middle Cretaceous Terrestrial Ecosystems (S. G. Lucas, J. I. Kirkland, and J. W. Estep, eds.). New Mexico Museum of Natural History and Science Bulletin, 14:177–181.
- SMITH, A. G., D. G. SMITH, AND B. M. FUNNELL. 1994. Atlas of Mesozoic and Cenozoic coastlines. Cambridge University Press, Cambridge, United Kingdom.
- ŠPINAR, Z. V. 1972. Tertiary frogs from Central Europe. W. Junk, The Hague, Holland.
- STEBBINS, R. C., AND N. W. COHEN. 1995. A natural history of amphibians. Princeton University Press, Princeton.
- TRUEB, L. 1973. Bones, frogs, and evolution. Pp. 65–127, in Evolutionary Biology of the Anurans, Contemporary Research on Major Problems (J. L. Vial, ed.). University of Missouri Press, Columbia.
- . 1993. Patterns of cranial diversity among the Lissamphibia. Pp. 255–343, in The Skull, Volume 2, Patterns of Structural and Systematic Diversity (J. Hanken and B. Hall, eds.). The University of Chicago Press, Chicago and London.
- . 1996. Historical constraints and morphological novelties in the evolution of the skeletal system of pipid frogs (Anura: Pipidae). Pp. 349–377, in The Biology of *Xenopus* (R. C. Tinsley and H. R. Kobel, eds.). Clarendon Press, Oxford, United Kingdom.
- . 1999. The Early Cretaceous pipid anuran, *Thoraciliacus*: redescription, reevaluation, and taxonomic status. Herpetologica, 55:139–157.
- VERGNAUD-GRAZZINI, C., AND R. HOFFSTETTER. 1972. Présence de Palaeobatrachidae (Anura) dans des gisements tertiaires français. Caractérisation, distribution et affinités de la famille. Paleovertebrata, 5:157–177.
- VERGNAUD-GRAZZINI, C., AND S. WENZ. 1975. Les Discoglossides du Jurassique supérieur du Montsec (Province de Lerida, Espagne). Annales de Paléontologie (Vertébrés) 61:19–36.

- WANG, Y., AND K. GAO. 1999. Earliest Asian discoglossid frog from Western Liaoning. *Chinese Science Bulletin*, 44:636–641.
- WERNER, C. 1994. Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk formation). *Berliner Geowissenschaftliche Abhandlungen*, 13:221–249.
- ZWEIFEL, A. 1956. Two pelobatoid frogs from the Tertiary of North America and their relationships to fossil and recent forms. *American Museum Novitates*, 1762:1–45.

Appendix—*Anatomical Terms and Abbreviations*

- ac—acetabulum  
 ac.b—acetabular border  
 a.ct—anterior cotyle  
 a.lm—anterior lamina  
 al.pr—alary process  
 a.tb—anterior tubercle  
 a.zy—anterior zygapophysis  
 btt—buttress  
 ce—centrum  
 cr.cr—crista cruris  
 cr.d—crista dorsalis (dorsal crest)  
 cr.f—crista femoralis  
 cr.pv—crista paraventralis  
 cr.v—crista ventralis  
 d.pr—dorsal prominence  
 ed.rs—edentulous rostrum  
 fs.cb—fossa cubitalis ventralis  
 fs.h—fossa for humeral condyle  
 fs.mx—fossa maxillaris  
 g—gutter  
 h.co—humeral condyle  
 il.bl—iliac blade  
 i.tb—interiliac tubercle  
 l.cr—lateral crest  
 l.gr—lateral groove  
 lm.h—lamina horizontalis  
 l.pt—ligament pit  
 m.bt—medial buttress  
 mx.f—maxillary facet  
 n—notch  
 n.f—nutrient foramen  
 no.c—notochordal canal  
 n.sp—neural spine  
 ol—olecranon  
 ol.s—olecranon scar  
 p.ac—pars acromialis  
 p.asc—processus ascendens (dorsal acetabular expansion)  
 p.co—posterior condyle  
 p.cor—processus coronoideus  
 p.ct—posterior cotyle  
 pd—neural arch pedicel  
 p.den—pars dentalis  
 p.des—processus descendens (ventral acetabular expansion)  
 p.gl—pars glenoidalis  
 p.pl—pars palatina  
 pr.pl—processus palatinus  
 p.zy—posterior zygapophysis  
 r—radius  
 r.e—raised edge  
 rs—rostrum  
 sc.bl—scapular blade  
 s.int—interglenoid sinus



s.mk—sulcus for Meckel's cartilage  
s.sc.s—attachment for suprascapular cartilage  
tb—tubercle on premaxilla  
tb.s—tuber superior (dorsal tubercle)  
tr.pr—transverse process  
u—ulna  
u.ep—ulnar epicondyle  
v.gr—ventral groove  
w.ex—waisting then expansion